



Yuzuncu Yil University
Journal of Agricultural Sciences
(Yüzüncü Yıl Üniversitesi Tarım Bilimleri Dergisi)

<https://dergipark.org.tr/en/pub/yyutbd>



ISSN: 1308-7576

e-ISSN: 1308-7584

Research Article

Morphological Plasticity and Genetic Diversity of *Eleusine indica* (L.) Gaertn. across Contrasting Disturbance Regimes Revealed by Chloroplast and Nuclear DNA Markers

Gunavathy SELVARAJH*¹, Tong PEI SIN²

^{1,2}Department of Agricultural and Food Science, Faculty of Science, Universiti Tunku Abdul Rahman, 31900
Kampar, Perak, Malaysia

¹<https://orcid.org/0000-0002-6041-6660>, ²<https://orcid.org/0000-0001-6603-9109>

*Corresponding author e-mail: gunavathy@utar.edu.my

Article Info

Received: 24.11.2025

Accepted: 27.07.2026

Online published: 20.10.2026

DOI: 10.29133/yyutbd.1828778

Keywords

Eleusine indica,
Genetic diversity,
psbA-trnH IGS marker

Abstract: *Eleusine indica* (L.) Gaertn. is one of the most aggressive and widely distributed weed species in tropical agroecosystems. It exhibits remarkable adaptability to diverse environmental conditions and anthropogenic disturbances. Its persistence across contrasting habitats is attributed to high reproductive capacity, strong competitive ability, and considerable phenotypic plasticity, making it a major challenge for sustainable weed management. Understanding the relationship between morphological variation and genetic diversity is essential for elucidating its adaptive strategies. This study examined the morphological variation and genetic diversity of *E. indica* across three contrasting habitats with different disturbance intensities using chloroplast and nuclear DNA markers. A total of 45 mature *E. indica* plants were collected for reproductive and vegetative morphological characterization, while 18 representative samples were selected for genetic diversity analyses. Reproductive traits including spike length, peduncle length, and seed length differed significantly among habitats ($p < 0.05$), indicating reproductive variation in response to environmental conditions. Genetic diversity analysis using the chloroplast *psbA-trnH* intergenic spacer revealed limited sequence variation, with only two haplotypes detected among the sampled populations. Similarly, inter-simple sequence repeat (ISSR) marker analysis showed no significant genetic differentiation among habitats ($p \geq 0.05$), with molecular variation occurring predominantly within populations. The combined findings from chloroplast and nuclear DNA markers indicate limited genetic structuring despite significant morphological variation across habitats, providing valuable information into the adaptive strategies of *E. indica* under contrasting disturbance regimes and supporting the development of effective weed management strategies.

To Cite: Selvarajh, G, Pei Sin, T, 2026. Morphological Plasticity and Genetic Diversity of *Eleusine indica* (L.) Gaertn. across Contrasting Disturbance Regimes Revealed by Chloroplast and Nuclear DNA Markers. *Yuzuncu Yil University Journal of Agricultural Sciences*, (1): 1828778. DOI: <https://doi.org/10.29133/yyutbd.1828778>

1. Introduction

Under increasing agricultural intensification and environmental change, weeds represent excellent examples of rapid evolutionary adaptation. *Eleusine indica* (L.) Gaertn., commonly known as goosegrass, is an annual grass weed belonging to the Poaceae family and is recognised as one of the most economically important and troublesome weed species worldwide (Selvarajh et al., 2017; Loddo

et al., 2020). It has been reported in more than 60 countries and infests at least 46 economically important crops, resulting in substantial yield losses in cereals, legumes, cotton, tobacco, and vegetables (Adoho et al., 2021). Its persistence across diverse habitats is largely attributed to its high reproductive capacity, prolonged emergence period, strong competitive ability, and remarkable adaptability to different environmental conditions (Ma et al., 2019; Loddo et al., 2020). Although native to Africa (Hamizan et al., 2021), *E. indica* is now widely distributed throughout tropical and subtropical regions, particularly in Africa, Asia, and South America (Ma et al., 2019). The weed exhibits considerable morphological variation depending on habitat conditions and can grow up to approximately 40 cm in height. Being monoecious and wind-pollinated, it readily establishes and reproduces in a wide range of agricultural and disturbed environments (Selvarajh et al., 2018).

The ecological success of *E. indica* is closely associated with its physiological adaptability and its ability to colonise open or disturbed habitats rapidly (Patel et al., 2023). It commonly occurs in vegetable farms, orchards, oil palm and rubber plantations, as well as along roadsides and wastelands in Malaysia (Chong et al., 2011). As a C₄ plant, *E. indica* exhibits high photosynthetic efficiency, superior water-use efficiency, and enhanced tolerance to drought and other environmental stresses, enabling it to persist under contrasting disturbance regimes. These adaptive characteristics allow the species to thrive in habitats subjected to varying degrees of anthropogenic disturbance, where continual environmental changes may promote the development of distinct ecotypes (Saritaş and Gürbüz, 2024; Dekker, 2011).

An individual *E. indica* plant is capable of producing up to 140 000 seeds, and its seeds are readily dispersed and established across different habitats, contributing to its persistence and invasiveness (Ma et al., 2019). The weed also exhibits prolonged germination and continuous seedling emergence, allowing populations to establish throughout the growing season. Variation in seed characteristics and plant morphology is often associated with reproductive success and environmental adaptation, reflecting the species' phenotypic plasticity under different habitat conditions (Hani et al., 2017). Morphological variation enables weeds to adjust their growth and reproductive characteristics in response to environmental variation, while genetic diversity provides the evolutionary basis for long-term adaptation to changing habitats (Fakhr et al., 2022). Consequently, integrating morphological and genetic information provides a more comprehensive understanding of weed adaptation than evaluating either component alone (Vauzia, et al., 2023). Despite the global importance of *E. indica*, studies simultaneously investigating morphological variation and genetic diversity across contrasting habitats remain limited, particularly in Malaysia.

Genetic diversity studies provide valuable insights into the evolutionary processes, adaptive potential, and population structure of weed species. Both chloroplast and nuclear DNA markers have been widely employed to investigate genetic variation because they provide complementary information on evolutionary relationships and population differentiation. While chloroplast genomes are relatively conserved and useful for phylogenetic and DNA barcoding studies, nuclear DNA markers generally exhibit higher levels of polymorphism, making them more suitable for population genetic analyses. Among chloroplast markers, the *psbA-trnH* intergenic spacer (IGS) has demonstrated high amplification success and informative sequence variation in many angiosperm species (Degtjareva et al., 2012). This region, located between the *psbA* and *trnH* genes, has been successfully applied in genera such as *Rhododendron*, *Dendrobium*, and *Compsonura* (Pang et al., 2012). Conversely, inter-simple sequence repeat (ISSR) markers amplify regions between microsatellite loci and are recognised as reliable, cost-effective, and highly polymorphic nuclear markers for assessing genetic diversity and population structure (Sarwat, 2012). ISSR markers have been successfully applied in several *Eleusine* species, particularly *E. coracana*, but their application in *E. indica* remains limited (Venkatesan et al., 2021). Therefore, integrating chloroplast and nuclear DNA markers provides complementary evidence for evaluating genetic diversity and population differentiation in *E. indica*.

Given these knowledge gaps, this study was designed to evaluate the morphological variation and genetic diversity of *E. indica* populations across three contrasting habitats with different levels of disturbance. The study hypothesised that populations inhabiting different disturbance regimes would exhibit morphological variation accompanied by detectable genetic differentiation. Specifically, the objectives were (i) to evaluate the reproductive variation of *E. indica* across contrasting habitats, and (ii) to assess genetic diversity using complementary chloroplast (*psbA-trnH*) and nuclear (ISSR) DNA markers. Integrating morphological observations with complementary molecular approaches provides

a more comprehensive understanding of the adaptive strategies of *E. indica*, thereby contributing valuable information for weed ecology, population genetics, and sustainable weed management.

2. Materials and Methods

2.1. Study area and habitat selection

Field sampling was conducted in Kampar, Perak, Malaysia. Three habitat types representing different levels of anthropogenic disturbance were selected: conventional farms (high disturbance), roadsides (moderate disturbance), and wastelands (low disturbance). Three locations were selected within each habitat type, and five mature *E. indica* plants were collected from each location, giving a total of 45 samples. GPS coordinates were recorded for all sampling sites. Habitat disturbance was classified based on land-use intensity following Bommarco et al. (2010) and Hantsch et al. (2013), where farms were characterised by frequent tillage and agrochemical application, roadsides by periodic vegetation management, and wastelands by minimal human disturbance.

2.2. Plant sample collection and morphological characterization

Forty-five mature *E. indica* plants with visible seedheads were collected using a mosaic sampling approach to minimise sampling bias associated with local gene flow and spatial clustering (Bommarco et al., 2010). Plant samples were cleaned before morphological assessment. Reproductive traits measured included the number of seedheads per plant, number of spikes per seedhead, spike length, peduncle length, seed weight, seed length, and seed width. Seed dimensions were measured using the Motic Camera Plus 2.0 imaging system (International Seed Morphology Association, 2020).

2.3. Plant morphological data analysis

Data were analysed using SAS OnDemand for Academics (SAS Institute Inc., Cary, NC, USA). A nested Analysis of Variance (ANOVA) was performed to detect statistically significant differences ($p < 0.05$) in reproductive traits across habitat types. Duncan's Multiple Range Test (DMRT) was used post hoc to differentiate between means. Reproductive trait data were classified into four quartile-based categories and used to generate a distance matrix with GenAlEx 6.51b2.

2.4 Genetic diversity assessment

2.4.1. DNA extraction

Young leaf tissues (0.03–0.05 g) were collected from each *E. indica* sample and preserved in silica gel prior to DNA extraction. Genomic DNA was extracted using the Biospin Plant DNA Extraction Kit according to the manufacturer's instructions. DNA quality and concentration were determined spectrophotometrically based on the A260/A280 ratio, and DNA samples were stored at -20°C until further analysis.

2.4.2. Chloroplast DNA amplification and sequencing

The chloroplast *psbA-trnH* intergenic spacer (IGS) was selected to evaluate genetic diversity using the universal primers described by Dwiati et al. (2023):

Forward: 5'-CGCGCATGGATTCACAAT-3'

Reverse: 5'-GTTATGCATGAACGTAAT-3'

PCR amplification was performed in a 50 μL reaction volume using a thermal cycler under standard amplification conditions. Amplified products were verified on 1.2% agarose gels before purification using the FavorPrep GEL/PCR Purification Mini Kit according to the manufacturer's instructions. Due to reagent limitations, 18 representative PCR products were submitted to Next Gene Scientific Sdn. Bhd. (Selangor, Malaysia) for Sanger sequencing. Raw sequences were edited using BioEdit version 7.2 and aligned with ClustalX2 to identify sequence variation among samples.

2.4.3. ISSR amplification

To complement the chloroplast DNA analysis, genetic diversity was further evaluated using an inter-simple sequence repeat (ISSR) marker. PCR amplification was carried out using ISSR primer

UBC-899 (5'-CATGGTGTGGTCATTGTTCCA-3') (Buczkowska and Dabert, 2011). PCR reactions were performed in a total volume of 50 μ L using 2 $\times$ GoTaq® Green Master Mix, ISSR primer, genomic DNA template, and nuclease-free water. Amplification was conducted using a MyCycler™ Thermal Cycler System (Bio-Rad) with an initial denaturation at 94 °C for 2 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 45 s, extension at 72 °C for 2 min, and a final extension at 72 °C for 5 min (Goh et al., 2010).

PCR products were separated on 3% agarose gels in 1 $\times$ TAE buffer using a 100 bp DNA ladder and visualised using a Molecular Imager® ChemiDoc™ XRS+ System (Bio-Rad). Gel images were captured using Image Lab™ software.

2.4.4. Genetic data analysis

For chloroplast DNA analysis, edited sequences were aligned using ClustalX2 to identify polymorphic sites and haplotypes among the sampled populations. For ISSR analysis, clear and reproducible bands were manually scored as binary data, where the presence and absence of a band were recorded as 1 and 0, respectively (van Steenderen, 2022). The binary matrix was analysed using GenAlEx version 6.5 to calculate genetic distances among samples. Principal Coordinates Analysis (PCoA) was performed to visualise genetic relationships, while Analysis of Molecular Variance (AMOVA) was conducted to evaluate the distribution of genetic variation within and among habitat types (Du et al., 2019).

3. Results

3.1. Reproductive morphological variation across habitats

Reproductive trait analysis of *E. indica* collected from various habitats revealed significant variation in several reproductive characteristics (Table 1). Among the seven traits evaluated, spike length, peduncle length, and seed length differed significantly among habitats ($p < 0.05$), whereas the number of seedheads per plant, number of spikes per seedhead, seed weight, and seed width did not vary significantly ($p > 0.05$).

Table 1. The reproductive morphology of *E. indica* in three different habitats

Habitats	Number of Seedheads/ Plant	Number of Spikes/ Seedhead	Spikes Length (cm)/ Seedhead	Peduncle Length (cm)/ Plant	Seed Weight (g) (100 seeds)	Seed Length (mm)	Seed Width (mm)
Farm	4.47 $\pm$ 2.97 ^a	5.13 $\pm$ 1.95 ^a	7.81 $\pm$ 1.64 ^a	20.09 $\pm$ 6.12 ^a	0.02 $\pm$ 0.01 ^a	1.14 $\pm$ 0.13 ^a	0.58 $\pm$ 0.08 ^a
Roadside	5.87 $\pm$ 4.06 ^a	4.33 $\pm$ 1.50 ^a	5.64 $\pm$ 1.46 ^b	12.32 $\pm$ 3.30 ^b	0.03 $\pm$ 0.01 ^a	1.29 $\pm$ 0.10 ^b	0.64 $\pm$ 0.07 ^a
Wasteland	6.27 $\pm$ 2.28 ^a	4.20 $\pm$ 0.97 ^a	7.32 $\pm$ 2.00 ^a	15.92 $\pm$ 6.02 ^b	0.03 $\pm$ 0.01 ^a	1.22 $\pm$ 0.14 ^{ab}	0.64 $\pm$ 0.08 ^a

The number of seedheads per plant ranged from approximately four to six across the three habitats, with wasteland populations showing the highest average. However, these differences were not statistically significant, suggesting that seedhead production remained relatively stable despite contrasting habitat conditions. Similar observations have been reported by Kerr et al. (2019), who found lower seedhead production in *E. indica* growing under well-maintained turfgrass conditions. Reduced reproductive output in managed agricultural systems may be associated with the application of growth regulators and increased competition with crops for light, nutrients, and water, causing plants to allocate more resources towards vegetative growth than seed production (Pant and Sah, 2020). Additional studies have also reported that resource availability and interspecific competition can substantially influence reproductive allocation in weedy species (Tang et al., 2022).

Although roadside populations exhibited the greatest variation in seedhead number, the differences were not significant. This variability may reflect the heterogeneous nature of roadside environments, where soil compaction, pollutant levels, water availability, and light intensity differ considerably over short distances. Such environmental fluctuations have been shown to influence flowering and reproductive development under stressful conditions (Asaduzzaman et al., 2022).

The number of spikes per seedhead remained relatively consistent among habitats, averaging between three and seven spikes per plant, which falls within the normal range reported for *E. indica* (Breedon, 2023). The stability of this trait may reflect the species' broad ecological adaptability and

continued gene flow among populations through seed dispersal facilitated by human activities and vehicles (Patel et al., 2023). In addition, the slightly higher number of spikes observed in farm populations may be associated with greater nutrient availability, particularly nitrogen, which promotes reproductive growth and inflorescence development (Anas et al., 2020; Tang et al., 2022).

Spike length differed significantly among habitats, with farm and wasteland populations producing longer spikes than roadside populations. Similar reductions in spike length under roadside conditions have been reported by Ikhajagbe et al. (2022). Roadside environments are frequently exposed to multiple stresses, including heavy metal contamination, air pollutants, soil compaction, and limited water availability, all of which may restrict nutrient uptake and reproductive development (Patel et al., 2023). Previous studies have also shown that spike development is closely associated with tillering patterns and spikelet formation, both of which can be influenced by environmental stress (Guo et al., 2018). Comparable responses have also been reported in other grass species exposed to environmental disturbance.

Peduncle length also varied significantly among habitats, with the longest peduncles recorded in farm populations and the shortest in roadside populations. Longer peduncles are generally associated with increased plant height and larger inflorescences under favourable growing conditions (Khalid et al., 2023). Fertile soils together with adequate nutrient availability in agricultural fields may therefore promote peduncle elongation (Chong et al., 2008; Buthelezi et al., 2023). In contrast, shorter peduncles observed in roadside populations may represent an adaptive response to water limitation and environmental stress, which reduce cell expansion and turgor pressure (Khalid et al., 2023). These findings suggest that peduncle length is a responsive morphological trait that varies according to habitat conditions.

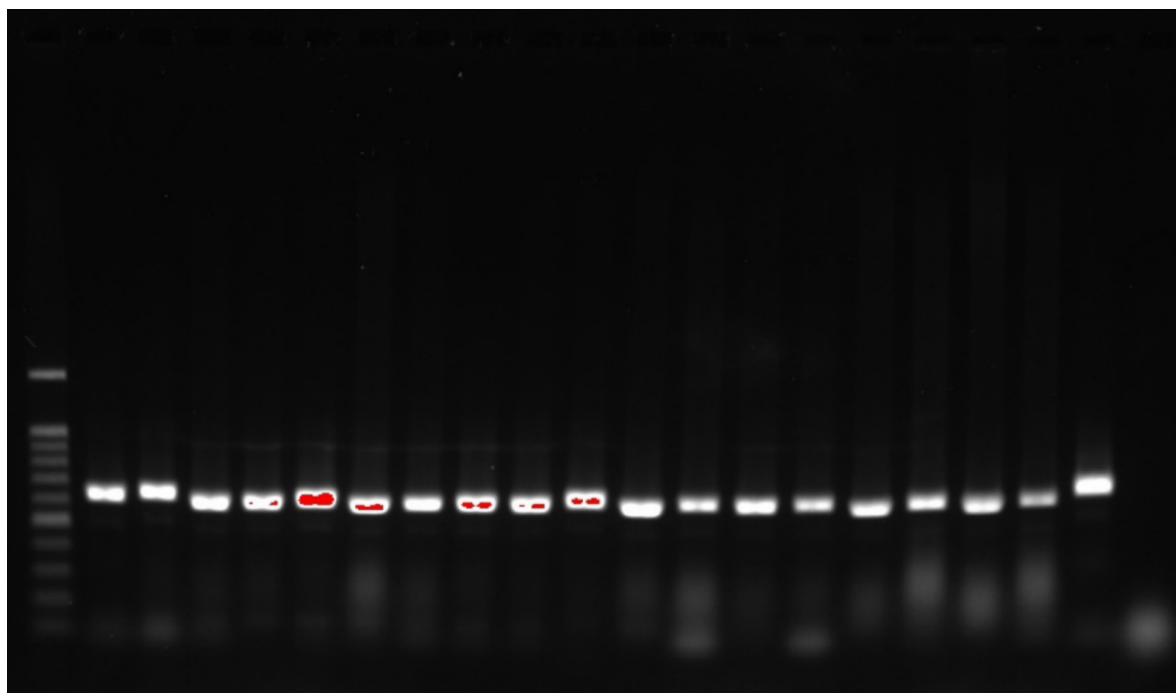
Seed weight and seed width did not differ significantly among habitats, indicating that these reproductive traits remained relatively conserved across populations. Their stability may reflect continuous gene flow among populations through seed dispersal by wind, water, animals, and human activities. The production of numerous small and lightweight seeds is also advantageous for dispersal and colonisation, contributing to the invasive success of *E. indica* (Hani et al., 2017). Similar observations have been reported for other invasive grass species, where seed size remained relatively stable despite contrasting environmental conditions (Sober and Ramula, 2013).

In contrast, seed length differed significantly among habitats, with roadside populations producing the longest seeds, followed by wasteland and farm populations. Variation in temperature, soil moisture, and light availability among habitats may contribute to these differences (Chuah et al., 2004). Larger seeds often provide greater reserves for seedling establishment under stressful conditions, potentially improving early growth and survival (Bullied et al., 2012). Several studies have similarly reported that seed size can increase under stressful environments as part of an adaptive reproductive strategy (Berger et al., 2017).

Overall, the results indicate that while several reproductive traits of *E. indica* remained relatively stable across habitats, spike length, peduncle length, and seed length responded to contrasting environmental conditions. These variations demonstrate the species' capacity to adjust its reproductive morphology across different habitats, which may contribute to its successful establishment and persistence in disturbed environments.

3.2. Genetic diversity analysis

Genomic DNA was successfully extracted from 18 representative *E. indica* samples collected from farm, roadside, and wasteland habitats. DNA concentrations ranged from 264.6 to 3757.5 ng μL^{-1} , with purity values between 1.92 and 2.09 (A260/A280), indicating DNA of sufficient quality for molecular analysis. Amplification of the chloroplast *psbA-trnH* intergenic spacer produced a single clear band of approximately 600–650 bp for all samples, confirming successful PCR amplification (Figure 1). Following sequence editing and trimming, the final sequence length was 542 bp (Figure 2).



ladder = 1 kb ladder.

Figure 1. PCR results of total 18 *E. indica* *psbA-trnH* IGS sequence from farm (F), roadside (R), and wasteland (W).

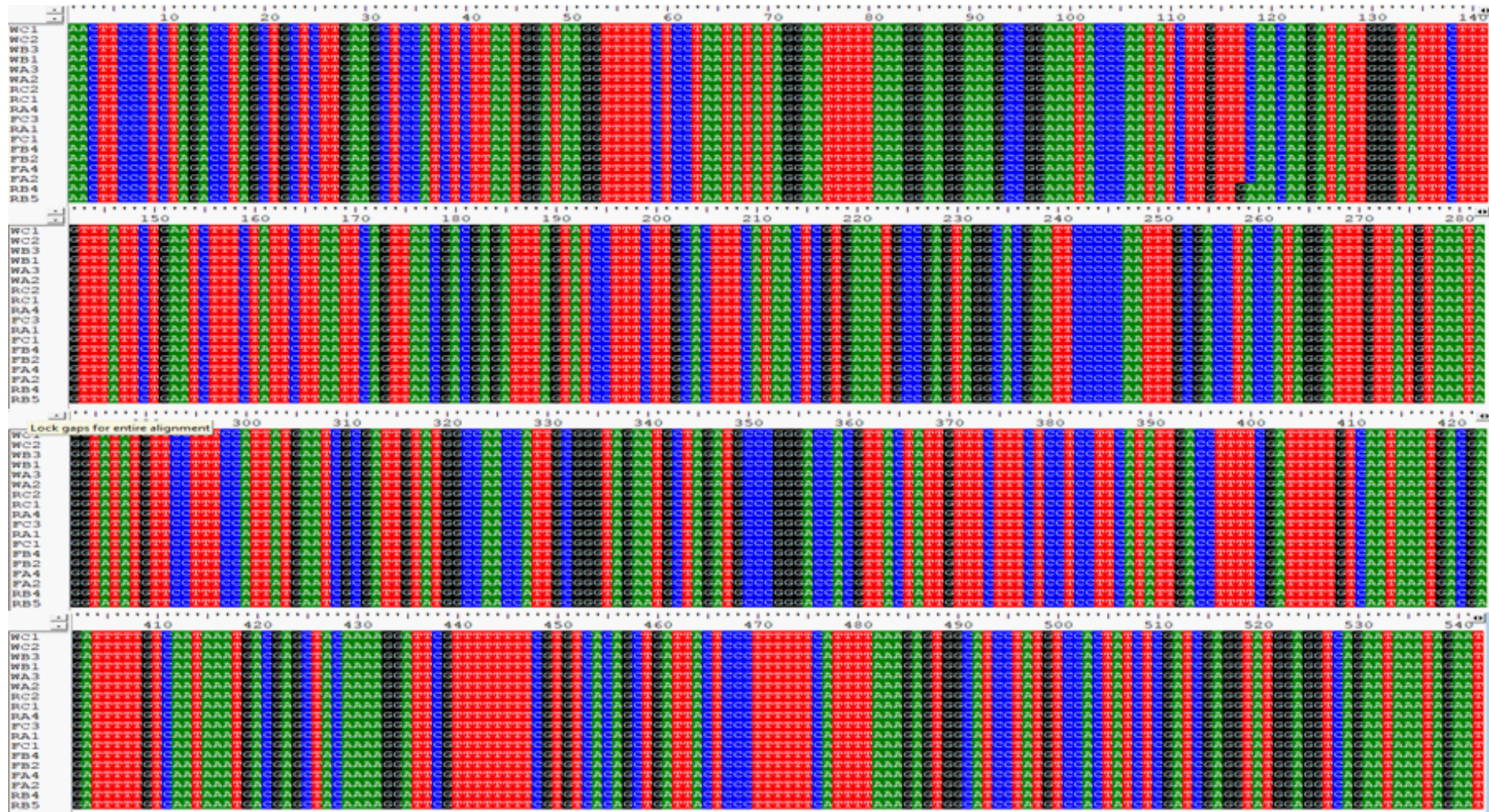
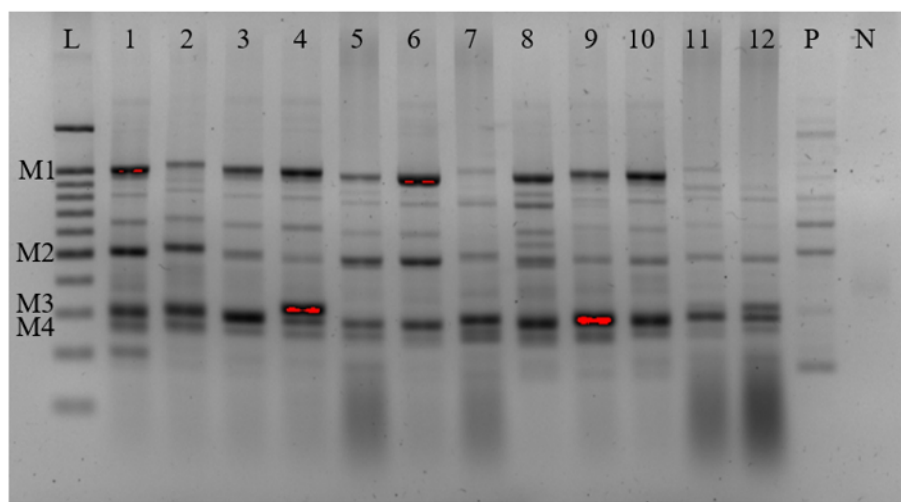


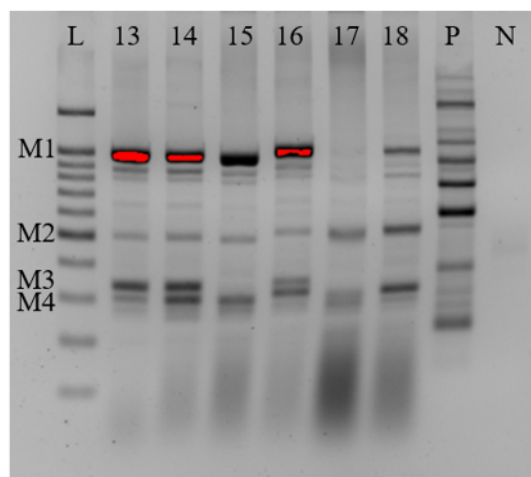
Figure 2. Complete sequence alignment of all *E. indica* samples from three habitat types- farm, roadside, and wasteland.

Sequence alignment revealed limited chloroplast sequence variation among the sampled populations. Two haplotypes were identified, differing only by nucleotide substitutions at positions 117 and 118 in two roadside samples (RB4 and RB5), whereas all remaining samples shared an identical haplotype. These findings indicate low chloroplast genetic variation and no clear genetic differentiation among the three habitat types.

To complement the chloroplast DNA analysis, genetic diversity was further assessed using the ISSR marker UBC-899. The primer generated four distinct bands ranging from approximately 200 to 1000 bp, and all amplified loci were polymorphic (100%) (Figure 3). Principal Coordinates Analysis (PCoA) based on ISSR binary data showed substantial overlap among individuals from the farm, roadside, and wasteland populations, with no distinct clustering according to habitat type (Figure 4). Similarly, Analysis of Molecular Variance (AMOVA) revealed no significant genetic differentiation among habitats ($\Phi_{IPT} = -0.058$, $p = 0.757$), with all molecular variation occurring within populations (100%) and no detectable molecular variation among populations (0%). Together with the PCoA, these findings indicate limited genetic differentiation among the sampled *E. indica* populations despite their occurrence in habitats with contrasting disturbance intensities.



(a)



(b)

Note: Lane L indicated 100 bp ladder, P indicated positive control, and N indicated negative control.

Figure 3. ISSR-PCR profiles of *E. indica* from (a) farm (L: 1 – 6), roadside (L: 7 – 12), and (b) wasteland (L: 13 – 18) based on ISSR UBC-899.

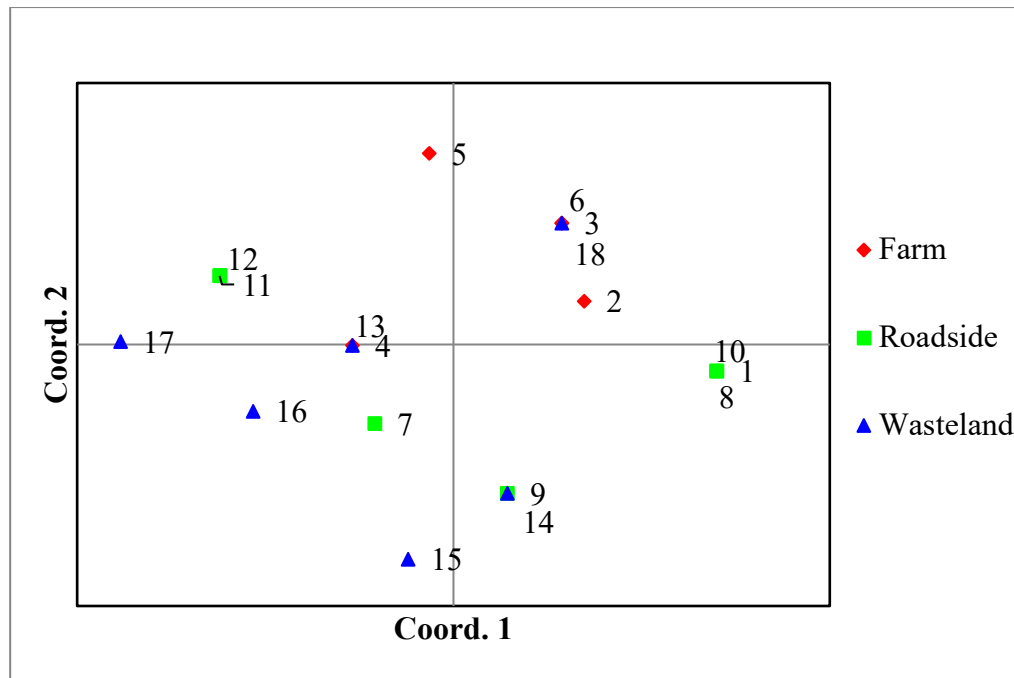


Figure 4. PCoA results for the ISSR profile of *E. indica* from three habitat types of farm, roadside, and wasteland.

The chloroplast and nuclear DNA markers consistently indicated limited genetic differentiation among *E. indica* populations despite their occurrence in habitats with contrasting disturbance intensities. The chloroplast *psbA-trnH* marker identified only two haplotypes, reflecting the relatively conserved nature of this intergenic spacer and its limited ability to resolve intraspecific variation. Similar limitations of the *psbA-trnH* region have been reported in other angiosperm species, where low sequence variability restricts discrimination among closely related taxa (Degtjareva et al., 2012).

Nevertheless, the marker remains useful for confirming species identity and evaluating broad chloroplast sequence conservation.

Although the ISSR marker detected complete polymorphism among the amplified loci, the overlapping PCoA distribution and non-significant AMOVA results indicate that the observed polymorphism did not translate into clear habitat-specific genetic differentiation. The predominance of molecular variation within populations rather than among habitats suggests that individuals from different habitats remain genetically similar (Drapikowska et al., 2020). This pattern may be attributed to frequent gene flow facilitated by effective seed dispersal through wind, water, animals, vehicles, and human activities, which promotes the exchange of genetic material among populations. In addition, the relatively small geographical scale of sampling within Kampar may have contributed to the high genetic similarity observed among populations by reducing opportunities for long-term genetic isolation.

The agreement between chloroplast and nuclear DNA markers provides greater confidence in the genetic patterns observed in this study. Despite significant variation in several reproductive morphological traits, both marker systems consistently indicated limited population genetic structuring across the three habitat types. These findings suggest that the observed morphological differences are more likely associated with phenotypic variation in response to environmental conditions than with substantial genetic divergence among populations. Nevertheless, the use of a single chloroplast marker and one ISSR primer may have limited the detection of finer-scale genetic variation. Future studies incorporating multiple ISSR primers, SSRs, SNPs, or genome-wide sequencing approaches across broader geographical regions are recommended to provide a more comprehensive assessment of the genetic diversity and population structure of *E. indica*.

Conclusion

Genetic analysis using the psbA-trnH intergenic spacer revealed limited chloroplast sequence variation among the sampled *E. indica* populations, with only two haplotypes identified across the three habitats. These findings suggest low detectable chloroplast genetic diversity within the sampled populations under the resolution of the psbA-trnH marker rather than the entire *Eleusine* genus. Future studies incorporating additional molecular markers or genome-wide approaches are recommended to provide a more comprehensive assessment of genetic diversity.

Ethical Statement

Ethical approval is not applicable for this study as it does not involve any human participants or animal experiments.

Acknowledgement

The authors gratefully acknowledge Universiti Tunku Abdul Rahman for providing the research facilities and financial support for this study. Special thanks are extended to Chin Yun Kuan and Vic Shuan Yap for their valuable technical assistance during sample collection and preliminary laboratory analyses.

Conflict of Interest

The authors declare there is no conflict of interest.

Artificial Intelligence Declaration

The authors declare that no generative artificial intelligence tools were used at any stage of the preparation of this manuscript, including the writing, editing, or refinement of the text, or the creation of any images, figures, graphics, tables, or related titles.

Funding Statement

Funding provided by Universiti Tunku Abdul Rahman.

Author Contributions

GS:- Writing and editing, TPS:- Conceptualization and editing.

Acknowledgements

The authors are grateful and thankful to Universiti Tunku Abdul Rahman for providing the funding and research facilities to conduct the work. We would like to express our sincere gratitude to Chin Yun Kuan and Yap Vic Shuan for their valuable contributions to the experimental work.

References

- Adoho, A. C. C., Zinsou, F. T., Olounlade, P. A., Azando, E. V. B., Hounzangbe-Adote, M. S., & Gbangboche, A. B. (2021). Review of the literature of *Eleusine indica*: Phytochemical, toxicity, pharmacological and zootechnical studies. *Journal of Pharmacognosy and Phytochemistry*, 10(3), 29–33.
- Anas, M., Liao, F., Verma, K. K., Sarwar, M. A., Mahmood, A., Chen, Z. L., Li, Q., Zeng, X. P., Liu, Y., & Li, Y. R. (2020). Fate of nitrogen in agriculture and environment: Agronomic, eco-physiological and molecular approaches to improve nitrogen use efficiency. *Biological Research*, 53(1), 1–20.

- Asaduzzaman, M., Wu, H., Koetz, E., Hopwood, M., & Shepherd, A. (2022). Phenology and population differentiation in reproductive plasticity in feathertop rhodes grass (*Chloris virgata* Sw.). *Agronomy*, 12(3), 736.
- Berger, J. D., Shrestha, D., & Ludwig, C. (2017). Reproductive strategies in Mediterranean legumes: Trade-offs between phenology, seed size and vigor within and between wild and domesticated *Lupinus* species collected along aridity gradients. *Frontiers in Plant Science*, 8, 548.
- Bommarco, R., Lönn, M., Danzer, U., Pålsson, K. J., & Torstensson, P. (2010). Genetic and phenotypic differences between thistle populations in response to habitat and weed management practices. *Biological Journal of the Linnean Society*, 99(4), 797–807.
- Breeden, G. K. (2023). *Goosegrass (Eleusine indica)*. Department of Plant Sciences, University of Tennessee Extension. <https://extension.tennessee.edu/publications/documents/w170.pdf>
- Buczkowska, K., & Dabert, M. (2011). The development of species-specific SCAR markers for delimitation of *Calypogeia* species. *Journal of Bryology*, 33(4), 291–299.
- Bullied, W. J., Van Acker, R. C., & Bullock, P. R. (2012). Microsite characteristics influencing weed seedling recruitment and implications for recruitment modeling. *Canadian Journal of Plant Science*, 92(4), 627–650.
- Buthlezi, L. G., Mavengahama, S., Sibiya, J., & Ntuli, N. R. (2023). Variation in shoot, peduncle and fruit growth of *Lagenaria siceraria* landraces. *Plants*, 12(3), 1–23.
- Chong, J. L., Wickneswari, R., Ismail, B. S., & Salmijah, S. (2008). Comparative growth studies of glyphosate-resistant and susceptible *Eleusine indica* (L.) Gaertn (goosegrass) biotypes from the Malaysian Peninsular. *Plant Protection Quarterly*, 23(2), 99–103.
- Chong, J. L., Wickneswari, R., Ismail, B. S., & Salmijah, S. (2011). Genetic diversity of glyphosate-resistant and glyphosate-susceptible *Eleusine indica* (L.) Gaertn (Poaceae) populations from Peninsular Malaysia. *Malaysian Applied Biology*, 40(2), 27–36.
- Chuah, T. S., Salmijah, S., Teng, Y. T., & Ismail, B. S. (2004). Changes in seed bank size and dormancy characteristics of the glyphosate-resistant biotype of goosegrass (*Eleusine indica* [L.] Gaertn.). *Weed Biology and Management*, 4(2), 114–121.
- Degtjareva, G. V., Logacheva, M. D., Samigullin, T. H., Terentieva, E. I., & Valiejo-Roman, C. M. (2012). Organization of chloroplast *psbA-trnH* intergenic spacer in dicotyledonous angiosperms of the family Umbelliferae. *Biochemistry (Moscow)*, 77, 1056–1064.
- Dekker, J. (2011). Evolution, natural selection and weedy adaptation. In *Evolutionary ecology of weeds* (pp. 48–55).
- Drapikowska, M., Buczkowska, K., Celka, Z., Szkudlarz, P., & Jackowiak, B. (2020). Genetic variability of *Anthoxanthum aristatum* Boiss. (Poaceae) at the non-native range limit. *Genetic Resources and Crop Evolution*, 67, 163–176.
- Du, X. H., Wang, H., Sun, J., Xiong, L., & Yu, J. (2019). Hybridization, characterization and transferability of SSRs in the genus *Morchella*. *Fungal Biology*, 123(7), 528–538.
- Dwiati, M., Dewi, T. A. N., & Susanto, A. H. (2023). Genetic diversity of cogongrass [*Imperata cylindrica* (L.) Raeusch] in Java Island based on *psbA-trnH* IGS. In *Proceedings of the 3rd International Conference on Sustainable Agriculture for Rural Development (ICSARD 2022)* (pp. 208–216). Atlantis Press.
- Fakhr, M. A., Mazrou, Y. S. A., Ellmouni, F. Y., Elsaied, A., Elhady, M., Elkelish, A., & Nour, I. H. (2022). Investigating the phenotypic plasticity of the invasive weed *Trianthema portulacastrum* L. *Plants*, 11(1), 77–96.
- Goh, W. L., Chandran, S., & Wong, K. M. (2010). Optimization of the ISSR-PCR system for the bamboos of economic importance. *Acta Horticulturae*, 875, 543–548.
- Guo, Z., Zhao, Y., Röder, M. S., Reif, J. C., Ganai, M. W., Chen, D., & Schnurbusch, T. (2018). Manipulation and prediction of spike morphology traits for the improvement of grain yield in wheat. *Scientific Reports*, 8(1), 1–10.
- Hamizan, Z. M. Z., Monica, S., Shean Yeaw, N., Zainab, N., Maili, S., & Fatimah, S. (2021). *Eleusine indica* for food and medicine. *Journal of Agrobiotechnology*, 12(2), 68–87.
- Hani, M., Lebazda, R., & Fenni, M. (2017). Variations of weeds seeds of species belonging to Poaceae on the basis of germination, production and morphological characteristics. *Advances in Research*, 10(3), 1–8.

- Hantsch, L., Bruelheide, H., & Erfmeier, A. (2013). High phenotypic variation of seed traits, germination characteristics and genetic diversity of an invasive annual weed. *Seed Science Research*, 23(1), 27–40.
- Ikhajiagbe, B., Chukwujama, C. A., & Ogwu, M. (2022). Intrinsic restoration of a ferruginous ultisol using goosegrass (*Eleusine indica* L. [Gaertn.]) obtained from different land use areas. *Journal of Natural Resources and Development*, 12, 1–18.
- International Seed Morphology Association. (2020). *Method for seed size measurement* (Version 1.0). ISMA Publication Guide.
- Kerr, R. A., Zhebentyayeva, T., Saski, C., & McCarty, L. B. (2019). Comprehensive phenotypic characterization and genetic distinction of distinct goosegrass (*Eleusine indica* L. Gaertn.) ecotypes. *Journal of Plant Science and Phytopathology*, 3(3), 95–100.
- Khalid, M. A., Ali, Z., Tahir, M. H. N., Ghaffar, A., & Ahmad, J. (2023). Genetic effects of GA-responsive dwarfing gene *Rht13* on plant height, peduncle length, internodal length and grain yield of wheat under drought stress. *Genes*, 14(3), 699.
- Loddo, D., Imperatore, G., Milani, A., Panozzo, S., Farinati, S., Sattin, M., & Zanin, G. (2020). First report of glyphosate-resistant biotype of *Eleusine indica* (L.) Gaertn. in Europe. *Agronomy*, 10(11), 1692–1703.
- Ma, X., Ma, Y., Wu, H., Ren, X., Jiang, W., & Ma, Y. (2019). Emergence timing affects growth and reproduction of goosegrass (*Eleusine indica*). *Weed Technology*, 33(6), 833–839.
- Pang, X., Liu, C., Shi, L., Liu, R., Liang, D., Li, H., Cherny, S. S., & Chen, S. (2012). Utility of the *trnH-psbA* intergenic spacer region and its combinations as plant DNA barcodes: A meta-analysis. *PLoS ONE*, 7(11), e48833.
- Pant, C., & Sah, S. K. (2020). Managing plant population and competition in field crops. *Acta Scientifica Malaysia (ASM)*, 4(2), 33–36.
- Patel, J., Hall, N. D., Harris, J. R., & McElroy, J. S. (2023). Morphological and metabolic differences between turfgrass and row-crop biotypes of goosegrass (*Eleusine indica*). *Crop Science*, 63, 1602–1612.
- Sarıtaş, A. G., & Gürbüz, R. (2024). Effects of hot water obtained by solar energy on the weeds *Convolvulus arvensis* L., *Setaria viridis* (L.) P. Beauv. and *Amaranthus retroflexus* L. *Yuzuncu Yıl University Journal of Agricultural Sciences*, 34(2), 346–353.
- Sarwat, M. (2012). ISSR: A reliable and cost-effective technique for detection of DNA polymorphism. In *Plant DNA fingerprinting and barcoding: Methods and protocols* (pp. 103–121). Humana Press.
- Selvarajh, G., Md Zain, N., & Seng, C. T. (2017). Effect of N fertilizer on the emergence and seedling growth of *Eleusine indica* in aerobic rice systems. *Plant Omics*, 10(5), 277–282.
- Selvarajh, G., Zain, N. M., Seng, C. T., & Aminudin, A. (2018). Herbicidal activity of pre and post emergent herbicide on control *Eleusine indica* in aerobic rice system. *Pakistan Journal of Botany*, 50(2), 511–515.
- Sober, V., & Ramula, S. (2013). Seed number and environmental conditions do not explain seed size variability for the invasive herb *Lupinus polyphyllus*. *Plant Ecology*, 214(6), 883–892.
- Tang, L., Zhou, Q. S., Gao, Y., & Li, P. (2022). Biomass allocation in response to salinity and competition in native and invasive species. *Ecosphere*, 13(1), e3900.
- van Steenderen, C. (2022). BinMat: A molecular genetics tool for processing binary data obtained from fragment analysis in R. *Biodiversity Data Journal*, 10, 77875–77889.
- Vauzia, V., Triana, B., Yeza, D. P., & Alti, R. P. (2023). Morphological characteristics and chlorophyll content of dominant weed leaves after peatland fires in oil palm plantation areas. *Yuzuncu Yıl University Journal of Agricultural Sciences*, 33(3), 389–396.
- Venkatesan, J., Ramu, V., Sethuraman, T., Sivagnanam, C., & Doss, G. (2021). Molecular marker for characterization of traditional and hybrid derivatives of *Eleusine coracana* (L.) using ISSR marker. *Journal of Genetic Engineering and Biotechnology*, 19, 1–12.