RESEARCH ARTICLE



Reducing methane emission from rainfed rice fields through utilizing amphibian rice cultivars

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ABSTRACT

Rainfed rice (*Oryza sativa* L.) fields are the largest rice contributor after irrigated rice fields in Indonesia. As land is vulnerable to climate change impacts, optimizing the productivity of rainfed lowland rice is carried out, among other things, by utilizing superior amphibian rice cultivars. On the other hand, rainfed rice fields whose irrigation depends on rainfall are seen as a source of greenhouse gas emissions, especially methane. The research objective was to determine methane emissions from rainfed rice fields by using amphibian rice cultivars. The field research was conducted in a randomized block design with seven amphibian rice cultivars and the lowland 'Ciherang' as control. The changes measured included plant growth, grain yield, methane flux, and greenhouse gas intensity (GHGI). The tested amphibian rice cultivars emitted methane lower by 2.2%-35.3% than 'Ciherang'. 'Inpari 34', 'Inpari 39', and 'Inpari 42' gave significantly lower GHGI values than other cultivars tested in rainfed rice fields, namely lower by 23.2%-31.5%, 8.1%-18.0%, 14.1%-23.4%, respectively. 'Inpari 34' is an amphibian cultivar that emits the lowest methane and releases the lowest CO₂ per ton of grain produced. The cultivars of 'Inpari 34', 'Inpari 39', and 'Inpari 42' are considered suitable and adaptive for rainfed rice fields.

Key words: Amphibian rice cultivar, carbon dioxide, grain yield, methane emission, Oryza sativa, rainfed rice fields.

INTRODUCTION

Human activities contribute to the increase of greenhouse gas (GHG) emissions into the atmosphere, which causes global warming and climate change. The impact of climate change occurs in various sectors, including the agricultural sector. The agricultural sector itself is responsible for providing food needs for the global, regional, national, and local population, which always increases every year. Apart from being vulnerable to the impacts of climate change, the agricultural sector is also a source of greenhouse gas emissions, especially carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) (Balakrishnan et al., 2018; Lynch et al., 2021). Indonesia's agricultural sector contributes as much as 5.7% of the total national GHG emissions (1 845 067 Gg CO_2e) (1 Gg = 10⁹ g) (Ministry of Environment and Forestry, 2021).

National methane emissions from the agricultural sector have increased from 39 940 Gg CO₂e (2000) to 46 407 Gg CO₂e (2019) (Ministry of Environment and Forestry, 2021). The mean global CH₄ concentration in the atmosphere in January 2016 was 1.84 part per million volume (ppmv) (Balakrishnan et al., 2018), which increased to 1.91 ppmv in March 2022 (Lan et al., 2023). The atmospheric CH₄ growth rate was 18.12 \pm 0.47 ppbv yr⁻¹ (Feng et al., 2023). Methane has a relatively short atmospheric lifetime (8-12 yr). In a 100-yr global

warming potential, one molecule of CH₄ traps about 28-34 times more heat than a molecule of CO₂ (IPCC, 2014; Fagodiya et al., 2022; Li et al., 2022; Saha et al., 2022).

Methane is one of the main GHGs in the agricultural sector which originates from lowland rice cultivation, livestock (manure management, enteric fermentation), biomass burning, and other cultivation practices (Balakrishnan et al., 2018). More than 90% of rice production is consumed in Asia, of which 27% is produced from rainfed rice fields (Wihardjaka et al., 2022). This means that rice fields have a significant contribution to the methane released into the atmosphere. The amount of methane emissions from rice fields depends on several factors, including rice plant varieties, soil type, water regime, soil organic matter content, fertilizer management, and soil properties (Balakrishnan et al., 2018; Feng et al., 2021; Wihardjaka et al., 2023). Soil types with high organic matter content generally emit high methane (Conrad, 2020). Intermittent irrigation emits less methane than continuous irrigation. The ideal conditions for methane formation occur at a redox potential of 150-200 mV (Tokarz and Urban, 2015; Saha et al., 2022). The deep placement of N fertilizer into the reductive layer of soil or applying N fertilizer containing sulfur (S) can reduce methane emissions from rice fields (Wihardjaka et al., 2023). Soil types with high oxidant content and acid reactions emit lower methane than alkaline soils with low oxidants.

The use of rice cultivars is one of the efforts to mitigate methane emissions from rice fields. Changing rice varieties can reduce CH₄ emissions by 40%-45% (Feng et al., 2021; Saha et al., 2022). Several factors influence the dynamics of CH₄ production and release from the rhizosphere of rice plants, including the morphological and physiological properties of rice plants, root systems, root exudation, and the abundance of microbes around the plant root zone (Feng et al., 2021; Soremi et al., 2023). The CH4 produced in the soils is emitted to the atmosphere through three different pathways - ebullition, diffusion, and plant-mediated transport (Saha et al., 2022). The rice plant plays an important role, as more than 90% of CH₄ is emitted from waterlogged soil to the atmosphere via aerenchyma cells (Kim et al., 2018; Saha et al., 2022; Habib et al., 2023; Soremi et al., 2023), although the mechanism for releasing CH_4 into the atmosphere is not yet clear (Kim et al., 2018). Methane formed in the rhizosphere of rice plants will be partially oxidized by methanotrophic microbes which are also present in plant roots. As much as 70% of the total CH₄ emissions will be released into the atmosphere through the aerenchyma tissue of rice plants (emissions), while 25% and 5% respectively through ebullition and diffusion (Mulyadi and Wihardjaka, 2014). Several cultivars of rice cultivated by Indonesian farmers, both irrigated and rainfed lowland, have a relatively low methane emission capacity with high yields, including 'Way Apoburu', 'Memberamo', 'Inpari 13', 'Dodokan', 'IR 64', 'IR 36', 'Cigeulis', 'Ciherang' (Setyanto et al., 2016; Wihardjaka et al., 2020a). Mitigation of methane emissions can be done by modifying the root system to utilize oxygen availability through aerenchyma and methanotrophs in the rhizosphere of rice plants (Rajendran et al., 2024).

Rainfed rice fields are the highest contributor to rice production after irrigated rice fields (Arianti et al., 2022). The area of rainfed rice fields in Indonesia is 29.4% of the total area of standard rice fields (7 463 950 ha) (Mulyani et al., 2022). As one of the agroecosystems that are vulnerable to the impacts of climate change, the use of adaptive rice varieties is recommended for rainfed rice fields to support food security. Exploiting varietal differences in CH₄ emissions has been proposed as a more cost-effective technique for decreasing CH₄ emissions (Soremi et al., 2023). The Ministry of Agriculture has released superior rice cultivars that are amphibious, where these cultivars can adapt to the rice fields in submerged or dry conditions. Amphibian comes from the word *amphi* which means double and *bios* which means life. Amphibian cultivars can be planted in rainfed rice fields with alternating wet-dry soil conditions. Amphibian rice cultivars in Indonesia are still limited in number. This is a challenge for breeders to produce superior cultivars that can adapt to drought conditions or immersion stress, by carrying out genotype crosses with these traits (Yullianida et al., 2014). Several amphibian cultivars that have been released by the Ministry of Agriculture, Indonesia are 'Limboto', 'Batutegi', 'Towuti', 'Situ Patenggang', 'Situ Bagendit', 'Inpari 10 Laeya', 'Inpago 4', 'Inpago 5', 'Inpago 6', 'Inpago 7', 'Inpago 8' and 'Inpago 9', with yield potentials ranging from 6.0 to 8.4 t ha⁻¹ dry grain (Thamrin et al., 2023).

The use of amphibian rice cultivars can contribute to increasing the cropping index in rainfed lowland areas and support food security. The concept of genotypes that emit less CH₄ without compromising yield is a compelling solution for fighting climate change and achieving food security goals (Soremi et al., 2023). Amphibian rice cultivars are thought to have well-developed aerenchyma which may promote CH₄ oxidation in the rhizosphere and reduce CH₄ emissions in rice fields (Li et al., 2022). However, the ability of these amphibian cultivars to release methane

into the atmosphere has not been further studied. Therefore, research is needed to determine the methane emissions of these high-yielding amphibious rice cultivars planted in rainfed rice fields.

MATERIALS AND METHODS

Experimental site

The field experiment was carried out in rainfed rice (*Oryza sativa* L.) fields in Pati Regency, Central Java Province, during the 2020 wet season. The experimental site was located at 6°45′ S and 111°10′ E. The soil at the experimental site was classified as Typic Endoaquepts which was dominated by silt (58.8%) followed by sand (29.3%), with a silt textural class. The chemical properties of the topsoil include slightly acidic soil reaction (pH 5.13), low organic C (3.2 g kg⁻¹), low total N (0.6 g kg⁻¹), low available P, low available K, and low cation exchange capacity (9.16 cmol kg⁻¹) (Table 1). Based on meteorological data (2009-2016), average annual rainfall is less than 1500 mm, mean daily solar radiation ranges from 389-559 MJ m⁻² mo⁻¹, and average maximum and minimum temperatures are 34.8 and 23.2 °C, respectively (Wihardjaka et al., 2022). The daily rainfall during the rice growth period is shown in Figure 1.

Soil properties	Method	Value	
Texture	Pipette		
Sand, %		29.3	
Silt, %		58.8	
Clay, %		11.9	
pH-H₂O	Electrode (1:2)	5.13	
Organic C, g kg ⁻¹	Walkley & Black	3.20	
Total N, g kg ⁻¹	Kjeldahl	0.60	
Available P, mg kg-1	Bray 1	13.0	
Cation exchange capacity, cmolc kg⁻¹	Ammonium saturation pH 7	9.16	
Exchangeable K, cmolc kg⁻¹	Ammonium saturation pH 7	0.04	
Exchangeable Na, cmolc kg ⁻¹	Ammonium saturation pH 7	0.10	
Exchangeable Ca, cmolc kg-1	Ammonium saturation pH 7	3.56	
Exchangeable Mg, cmolc kg⁻¹	Ammonium saturation pH 7	0.41	

Table 1. Physical and chemical properties of initial soil in the experimental site.

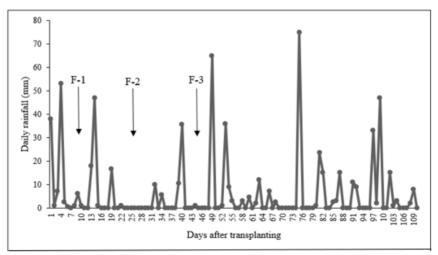


Figure 1. Daily rainfall during rice growth period at rainfed rice field. F1: Fertilizer applied at 7 d after transplanting; F2: at maximum tillering growth phase; F3 at panicle initiation growth phase.

Experimental design

The experiment was arranged in a randomized block design, with three replicates and eight treatments of rice cultivars, which included seven amphibian rice cultivars ('Inpago Unsoed 1', 'Inpago 9', 'Inpago 10', 'Inpari 34 Agritan', 'Inpari 39 Agritan', 'Inpari 42 GSR', 'Situ Bagendit') and 'Ciherang' as a baseline variety. 'Ciherang' is a cultivar of paddy rice popularly cultivated by Indonesian farmers and is considered one of the superior varieties with low methane emission capacity (Pramono et al., 2020; Wihardjaka et al., 2020b).

Cultural practices

The soil was perfectly tilled using a plow and leveled, and plots were made with a size of 5 m \times 6 m. Simultaneously with soil preparation, farmyard manure 2.5 t ha⁻¹ was incorporated into the soil in each plot. According to the treatment, two seedlings of rice varieties were transplanted from the seedbed after 3 wk of age on 22 February 2020. Seedlings were planted with a spacing of 20 cm \times 20 cm in each plot.

The dosage of fertilizer used in rice plants was 120 kg N, 20 kg P, and 50 kg K per hectare (ha). The N fertilizer was applied at three stages, namely 1/3 N at 7 d after transplanting (DAT), 1/3 N at maximum tillering growth phase, and 1/3 N at panicle initiation growth phase. The P fertilizer was applied at once at 7 DAT, and K fertilizer was applied in two growth phases, namely 1/2K at 7 DAT, and 1/2K at panicle initiation.

Plant maintenance was carried out intensively. Weed control was done manually at least twice, namely at active tillering and maximum tillering, respectively. The water height in the experimental plots should be kept in stagnant conditions (± 2 cm) when daily rainfall is enough. Control of other major pests was carried out by spraying insecticides according to the types of pests that develop in the field. The plants were harvested on 18 May 2020 for 'Inpari 34', 2 June 2020 for 'Inpago Unsoed 1', 'Inpago 9', 'Inpari 39', 'Situ Bagendit', and 12 June 2020 for 'Ciherang', 'Inpago 10', 'Inpari 42'.

Parameter observed

The variables measured included agronomic parameters including plant height, number of tillers, yield components (filled grain, empty grain, 1000-grain weight), grain yield, methane flux, and greenhouse gas intensity (GHGI). Plant height and number of tillers were measured from 12 hills per plot at maximum and productive tillers. Yield components were measured from 3 hills per plot. The grain yield was measured from an area harvest of 3 m × 4 m.

The determination of methane flux began with gas sampling using the closed chamber method, where air sampling was carried out in the critical growth phase (20, 35, 55, 70, and 85 DAT). Gas samples were taken at 5 min intervals at 5, 10, 15, and 20 min to determine the CH₄ flux. Gas samples were taken with a 10 mL volume syringe on the chamber surface. Simultaneously with air sampling, the temperature in the containment and head space height were recorded. Air samples were injected into a gas chromatograph equipped with a Porapak K column and a flame ionization detector (FID) to determine the concentration of CH₄ gas. The CH₄ flux was calculated using the formula used by Soremi et al. (2023) as follows:

$$F_{\text{methane}} = \frac{\Delta C}{\Delta t} \times \frac{v}{A} \times \rho \times \frac{273}{(273 + T)}$$
(1)

where $\Delta C/\Delta t$ is the concentration change (mg CH₄ kg⁻¹ h⁻¹), V is chamber volume (m³), A is chamber area (m²), ρ is gas density (0.717 kg m⁻³ at 0 °C), and T is the mean air temperature inside the chamber (°C).

Greenhouse gas intensity (GHGI) was used to measure the GHG emissions per unit of grain production (Feng et al., 2021) as follow:

GHGI (t CO₂ equivalent t⁻¹ grains) = GWP/grain yields (2)

Based on IPCC (2014), the global warming potential (GWP) of CH_4 is computed from 28 × one CO_2 molecule.

Data analysis

The collected data was analyzed statistically using the Minitab program (Minitab, State College, Pennsylvania, USA) to get an ANOVA. If ANOVA is significant, a further test is done using honest significant difference (Tukey test) at p < 0.05 probability level to determine the mean significance among treatments.

RESULTS AND DISCUSSION

Rice growth and grain yield

Climate anomalies due to the impact of climate change also occur in the agroecology of rainfed rice fields where wet-dry conditions occur one after another and cannot be predicted accurately. The introduction of high-yielding cultivars that can adapt to submerged or dry soil conditions is urgently needed for rainfed farmers, in addition to other adaptive technologies. Plant growth and grain yield of the rice cultivars studied were generally significant, namely for the variables plant height, number of productive tillers, number of grains per panicle, and grain yield which were significant at p < 0.05, while the variables for the number of maximum tillers and 1000-grain weight were significant at p < 0.01 (Table 2). The plant height of 'Inpago' was generally higher than that of the 'Inpari', 'Ciherang', and 'Situ Bagendit', but the number of maximum tillers was relatively lower.

The grain yield of 'Situ Bagendit' was the lowest compared to other cultivars in the 2020 cropping season. The highest grain yield was shown in 'Inpago 9', which appeared to have the highest 1000-grain weight compared to the other cultivars (Table 2). In general, grain yields of all cultivars tested in rainfed lowland areas were still lower than the potential yields (Thamrin et al., 2023). Therefore, the application of adaptive technology is necessary to optimize the ability of each of these cultivars to provide optimum productivity.

In general, the cultivars studied in rainfed rice fields gave better yields than the average yield of rainfed rice which ranged from 3.81-4.36 t ha⁻¹ (research results by Boling et al., 2007). Varieties with drought-resistant characteristics save the generative phase from drought stress, where drought stress in this phase can significantly reduce grain yield (Mudhor et al., 2022). Drought conditions trigger biological stress that disrupts physiological and functional activities in plants, which begins with the closure and narrowing of stomata. These conditions reduce the rate of photosynthesis and the formation of carbohydrates in plant products (Mudhor et al., 2022). Plants are resistant to drought as indicated by the high levels of total sugar compounds and proline which can protect cells from damage due to changes in osmotic pressure. When the osmotic potential pressure is low, these compounds act as guardians of cell turgor and root growth (Mudhor et al., 2022).

	Plant	Tillers	per hill		Grains per ŀ	nill	Weight	
Rice cultivar	height	Maximum	Productive	Total	Filled	Unfilled	of 1000- grain	Grain yield
	cm	Nr	hill-1 ———		— Nr hill-1-		g	t ha-1
Ciherang	114ª	14 ^{ab}	10 ^{bc}	1267 ^b	952ªb	316°	27.40°	5.54ªb
Inpago Unsoed 1	132 ^b	12 ^{cd}	8 ^{de}	1236 ^b	756 ^b	480 ^{bc}	27.10 ^c	4.65°
Inpago 9	142ª	9°	6 ^f	1321 ^b	816 ^b	506 ^b	31.33ª	5.95ª
Inpago 10	130 ^b	9°	7 ^{ef}	1987ª	1074 ^{ab}	913ª	27.03°	4.98 ^{bc}
Inpari 34	141ª	13 ^{ab}	9 ^{cd}	1155 ^b	833 ^b	323°	28.33 ^b	5.03 ^{bc}
Inpari 39	111 ^{cd}	12 ^{bc}	11 ^b	1188 ^b	917ªb	271°	27.23°	5.11 ^{bc}
Inpari 42	112 ^{cd}	10 ^{de}	10 ^{bc}	1856ª	1261ª	594 ^b	24.50 ^d	5.25 ^{bc}
Situ Bagendit p-value	107ª •	15ª **	12ª •	1259 ^b	785 ^b	474 ^{bc}	27.00°	3.83 ^d

Table 2. Growth and grain yield of amphibian rice cultivars. Means in the same column followed by the same letter do not differ significantly according to Tukey test 0.05. *Significant at p < 0.05, **significant at p < 0.01.

Methane flux

Methane fluxes from all cultivars tested generally increased at 33 and 55 d after transplanting (DAT) and decreased after the plants were 55 DAT (Figure 1). At the end of plant growth (85 DAT), the CH₄ flux of 'Ciherang' and 'Inpari 34' showed a steady downward curve, but other cultivars such as 'Situ Bagendit', 'Inpari Unsoed 1', 'Inpago 9', 'Inpago 10', 'Inpari 39', and 'Inpari 42' experienced an increase in CH₄ flux (Figure 2). Methane fluctuations tend to be higher in the maximum tillering phase, it is important to remember that methane emissions can also occur during the grain filling or generative phase. According to Gogoi et al. (2008), methane emission is reported to be high at the active tillering, flowering, and ripening stages of the crop under

continuously flooded conditions. Methane fluctuations in rice vegetative growth are the result of complex interactions between environmental factors, plant biology, and agricultural practices. In the maximum tillering phase, root growth and the root system of rice plants are in a stage of rapid development. This condition can trigger higher anaerobic respiration activity in the rhizosphere of rice plant roots where a substrate is available for methanogenic activity originating from root exudates which can cause higher methane release into the atmosphere. Soil microbial composition and the presence of methanogenic microbes can differ between the vegetative and generative phases. Different environmental conditions and resources during the two phases can affect the presence and activity of these microbes.

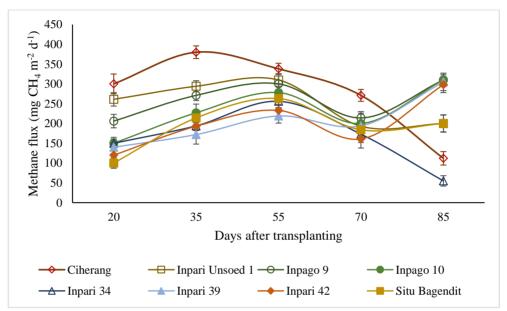


Figure 2. Methane flux at critical growth stages of amphibian rice cultivars.

The methane flux observed in 'Inpari 34' and 'Situ Bagendit' was relatively lower than the other cultivars studied in the five observations (Figure 2). This means that these cultivars have certain factors that can inhibit methanogenic microbial activity in the rhizosphere of rice plants, even though flooded conditions occur during plant growth as indicated by sufficient daily rainfall for rice plant growth (Figure 1).

Methane emissions and greenhouse gas intensity (GHGI) are significant at p < 0.01. 'Ciherang' is used as a comparison, as it can release methane into the atmosphere at a relatively low rate. This trait was inherited from the parent IR 64 (Thamrin et al., 2023), which is also a rice cultivar with low methane emissions (Setyanto et al., 2016). Amphibian rice cultivars emit methane significantly lower by 2.2%-35.3% than 'Ciherang' (Table 3). 'Inpari 34', 'Inpari 39', 'Inpari 42', and 'Situ Bagendit' provide lower methane emissions than 'Inpago 10', 'Inpago Unsoed 1', 'Inpago 9', and 'Ciherang'. Amphibian rice cultivars usually grow in land conditions that are not always flooded, so these cultivars have the character of being able to utilize more oxygen in the rhizosphere than irrigated lowland rice (such as 'Ciherang'). Based on the Pearson correlation test, the correlation coefficient between CH₄ flux and root weight and biomass weight in the heading growth phase were -0.239 and -0.128 respectively (data not shown), meaning that the correlation between these variables appeared weak and negative. The availability of oxygen around the roots of amphibian cultivars can inhibit the activity of methanogens that produce methane and increase the activity of methanotrophs. Methanotrophs in rice roots can increase the rate of CH₄ oxidation, where CH₄ oxidation is highly dependent on the availability of oxygen in the rhizosphere supplied through the rice aerenchyma (Rajendran et al., 2024).

Rice cultivars	CH₄ emission	Grain yield	GHGI
	kg ha ⁻¹ season ⁻¹	t ha-1	t CO₂-e t⁻¹ grains
Ciherang	224ª	5.54ªb	1.00 ^b
Inpago Unsoed 1	217 ^{ab}	4.65°	0.99 ^b
Inpago 9	219 ^{ab}	5.95ª	0.99 ^b
Inpago 10	195 ^{bc}	4.98 ^{bc}	1.10ª
Inpari 34	145 ^d	5.03 ^{bc}	0.76 ^e
Inpari 39	173 ^{cd}	5.11 ^{bc}	0.91°
Inpari 42	167 ^d	5.25 ^{bc}	0.85 ^d
Situ Bagendit	162 ^d	3.83 ^d	1.11ª
p-value	**	**	••

Table 3. Methane emission and greenhouse gas intensity (GHGI) from some amphibian rice cultivars in rainfed rice fields. Means in the same column followed by the same letter do not differ significantly according to Tukey test 0.05. ^{**}Significant at p < 0.01.

The GHGI value is low, and every ton of grain produced gives low methane emissions. GHGI values can be used to determine rice cultivars that produce high grain while contributing to low greenhouse gas emissions. 'Situ Bagendit', 'Inpago Unsoed 1', and 'Inpago 10' gave GHGI values relatively high. Those cultivars reflected the lower methane emission and grain yield. The lower grain yields and CH₄ emissions showed that several of these tillers were unproductive, and the high tiller numbers did not translate to high CH₄ emissions (Soremi et al., 2023).

'Inpari 34', 'Inpari 39', and 'Inpari 42' gave significantly lower GHGI values than the other cultivars tested in rainfed lowland areas (Table 3), namely lower by 23.2%-31.5%, 8.1%-18.0%, 14.1%-23.4%, respectively. 'Inpari 34' and 'Inpari 42' are amphibious cultivars that emit the lowest methane, also releasing the lowest CO₂ per ton of grain they produce. Rice crops respond directly to available CO₂ through photosynthesis and stomatal conductance, which hence promotes crop yield (Lv et al., 2020). The CO₂ has a significant effect on stomata opening, so rice plants can optimize CO₂ absorption (Sugiura et al., 2024). The lowest GHGI value was shown by 'Inpari 34', where this cultivar besides being amphibian is also claimed to be a cultivar resistant to high salinity. It is possible that the resistance to high salt content also contributes to the inhibition of methanogenic microbial activity in forming methane in the roots of rice plants. The GHG emissions usually decrease with increased soil salinity (Fagodiya et al., 2022). This cultivar is considered suitable for rain-fed paddy fields which experience alternating wet-dry changes every year.

CONCLUSIONS

The use of amphibian rice cultivars can be considered as an effort to mitigate methane emissions in rainfed rice fields. The tested amphibian rice cultivars emitted methane lower by 2.2%-35.3% than 'Ciherang'. The lowest methane emissions were shown in 'Inpari 34', 'Situ Bagendit', and 'Inpari 42'. The grain yield of the amphibian rice cultivars was relatively lower than that of the 'Ciherang'. 'Inpari 34', 'Inpari 39', and 'Inpari 42' gave significantly lower greenhouse gas intensity (GHGI) values than the other cultivars tested in rainfed lowland areas. 'Inpari 34' and 'Inpari 42' are amphibious cultivars that emit the lowest methane, also releasing the lowest CO₂ per ton of grain they produce. These cultivars are considered suitable for being developed in rainfed rice fields.

Authors contribution

Conceptualization: A.W., E.S.H., M.T.S. Methodology: A.W., E.Y., T.A.A., E.S.H. Software: A.W., E.S.H., T.A.A. Validation: A.W. Formal analysis: A.W., E.S.H., Y.H., S.J. Investigation: A.W., E.Y., T.A.A. Resources: A.W., E.S.H. Data curation: A.W., E.S.H. Writing-original draft: A.W., E.S.H., M.T.S., E.Y., Y.H., S.J. Writing-review & editing: A.W., E.S.H., M.T.S., T.A.A., Y.H., S.J. Visualization: A.W., E.S.H. Supervision: A.W. Project administration: A.W., T.A.A. Funding acquisition: A.W., T.A.A. All authors reviewed the final version and approved the manuscript before submission.

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