



Evaluating the Agronomic Response of Rice Genotypes to Diverse Crop Rotation Sequences

Bela Tri Wijayanti¹, Taufan Alam², Budiastuti Kurniasih², Taryono², Wilujeng Hidayati³

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ABSTRACT

Background: Intensive rice monoculture in Indonesia drives yield stagnation and progressive land degradation. This study evaluated newly developed breeding lines across contrasting crop rotation sequences to identify synergistic genotype-environment combinations that mitigate monoculture-induced degradation.

Methods: The experiment was conducted at the Agrotechnology Innovation Center, Universitas Gadjah Mada, Yogyakarta, Indonesia. A factorial randomized complete block design (RCBD) evaluated two factors: 12 rice genotypes (10 promising breeding lines and two commercial controls) and three rotation environments, namely rice-rice-rice (R-R-R), maize-maize-rice (M-M-R) and vegetable-vegetable-rice (V-V-R).

Result: ANOVA showed significant $G \times E$ interactions for grain number per panicle ($p = 0.0038$), harvest index ($p < 0.0001$) and number of productive tillers ($p = 0.0229$). The M-M-R and V-V-R rotations significantly increased the harvest index to 0.34 and 0.35, respectively, compared with 0.22 under R-R-R monoculture ($p < 0.0001$). Genotype GM 8 showed superior performance, achieving a maximum harvest index of 0.51 in V-V-R and 299.33 grains per panicle in M-M-R, whereas Inpari 30 Ciherang Sub 1 recorded the lowest efficiency (harvest index 0.17). Switching to maize- or vegetable-based rotations with suitable genotypes, such as GM 8, is therefore a viable approach to improving yield attributes.

Key words: Breeding lines, Cropping sequences, *Oryza sativa*, Soil legacy effects.

INTRODUCTION

Rice (*Oryza sativa* L.) is a pivotal tropical cereal crop that meets the primary dietary and nutritional requirements of populations in developing nations (Kaur *et al.*, 2022). However, sustaining its production faces severe challenges due to climate change and intensifying competition for finite land and water resources, driven by demographic and industrial expansion (Khush, 2005). In Indonesia, national rice production has shown only limited growth in recent years (BPS, 2024) and this vulnerability threatens long-term food security, particularly with the national population projected to surpass 320 million by 2050 (Rahman *et al.*, 2023). While external climate fluctuations and shrinking arable areas continuously degrade land quality (Suryani *et al.*, 2021; Widyawati *et al.*, 2025), a critical yet overlooked internal driver of this widespread yield stagnation remains the long-standing practice of intensive rice monoculture.

Rooted in the green revolution, intensive monoculture prioritizes chemical fertilizers and pesticides at the expense of ecological stability. Year-round irrigation and continuous cropping cause significant edaphic degradation, including subsoil compaction, nutrient imbalances and a sharp decline in biodiversity (Yi *et al.*, 2020), while depleting nitrogen, phosphorus and potassium reserves and driving carbon migration to deeper soil layers (Sun *et al.*, 2021). Heavy reliance on agrochemicals, combined with insufficient crop diversity, suppresses beneficial nitrogen-fixing and phosphorus-solubilizing bacteria, leading to rhizosphere microbial dysbiosis and the accumulation of allelopathic compounds (Ma *et al.*, 2022). This breakdown

¹Department of Agribusiness, Vocational School, Universitas Sebelas Maret. Jl. Ir. Sutami 36A Surakarta 57126, Central Java, Indonesia.

²Department of Agronomy, Faculty of Agriculture, Universitas Gadjah Mada, Bulaksumur-55281, Yogyakarta, Indonesia.

³Department of Agrotechnology, Faculty of Agriculture, Universitas Jendral Soedirman, Purwokerto, Central Java Indonesia.

Corresponding Author: Bela Tri Wijayanti, Department of Agribusiness, Vocational School, Universitas Sebelas Maret. Jl. Ir. Sutami 36A Surakarta 57126, Central Java, Indonesia.
Email: belawijayanti@staff.uns.ac.id

ORCID: 0000-0001-9657-4639, 0000-0002-2234-6796, 0000-0001-7476-5573, 0000-0003-1425-969X, 0000-0001-9800-3768

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of the soil-plant-microbe feedback loop disrupts the ecological balance necessary for sustained land productivity.

Systemic edaphic degradation induced by continuous monoculture can be effectively mitigated through crop rotation. Integrating diverse crop species into the rotational matrix enriches soil microbial communities by stimulating the proliferation of beneficial bacteria and fungi (Liu *et al.*, 2023), consistent with Yang *et al.* (2021), who found that crop diversification promotes soil richness, biodiversity and

microbial biomass. Rotation further promotes nutrient cycling, suppresses pathogens and regulates nitrogen-metabolism genes (Chen *et al.*, 2025), enhances agroecosystem resilience (Shah *et al.*, 2021) and regulates phosphorus availability through residue mineralization (Yang *et al.*, 2024). Alternating rice with upland crops also suppresses soil-borne pathogens, notably reducing *Hirschmanniella* spp. abundance (Nguyen *et al.*, 2020). Comparable assessments in tropical Asia confirm that rice- and maize-based sequences generate measurably different soil quality profiles (Nguyen *et al.*, 2025), while the depth-wise distribution of available N, P and K differs markedly among rice-based rotations (Kumar *et al.*, 2024). Maximizing productivity, therefore, requires strategically matching genotypes to the specific environmental conditions created by each rotation sequence.

Despite the acknowledged benefits of rotation, a significant research gap remains in understanding specific genotype-by-environment ($G \times E$) interactions within these systems. Contemporary research predominantly examines soil health or varietal stability in isolation (Pandey *et al.*, 2020; Wu *et al.*, 2024), leaving a knowledge gap regarding the phenotypic plasticity of specific rice genotypes in relation to nutrient fluxes associated with different rotation sequences. The present study employs three sequences representing contrasting agronomic settings: R-R-R as a control for continuous anaerobic monoculture and M-M-R and V-V-R, which incorporate aerobic periods and distinct residual nutrient profiles, particularly following intensive horticultural fertilization. Using a multi-environment trial approach, the study assesses the agronomic performance and production potential of promising new breeding lines across these sequences to identify robust, high-yielding candidates and provide a strategic pathway for restoring soil health in Indonesia.

MATERIALS AND METHODS

This research was conducted at the Agrotechnology Innovation Center, Universitas Gadjah Mada, Yogyakarta, Indonesia, under environmental conditions averaging 26.28°C, 66.26% relative humidity and approximately 727 mm rainfall, with uniform supplemental irrigation. Baseline soil analysis revealed inherent spatial variation in soil texture across the experimental site, with loam in the blocks designated for the R-R-R and M-M-R sequences and sandy loam in the blocks allocated to the V-V-R system. The three cropping sequences were implemented based on a one-year continuous land-use history, while the intensive agronomic evaluation of the genotypes was conducted during a single cropping season. Prior to transplanting, baseline edaphic profiling established distinct nutrient legacies across the three sequences: R-R-R (loam; pH 6.27; 0.32% total N (Kjeldahl); 36.12 ppm P (Olsen); 0.71 meq% K (25% HCl extraction)), M-M-R (loam; pH 7.62; 0.20% total N; 45.51 ppm P; 0.52 meq% K) and legume-inclusive V-V-R (sandy loam; pH 7.48; 0.33% total

N; 26.45 ppm P; 0.34 meq% K). These heterogeneous soil chemical and physical properties provided contrasting environmental matrices for evaluating $G \times E$ interactions.

The experiment was arranged in a factorial randomized complete block design (RCBD) with three replications. The first factor comprised 12 genotypes, including 10 promising breeding lines (V11, GM 2, GM 8, GM 28, Mutant Lampung Kuning, Mutant Rojolele 30 Pendek, Mutant Rojolele 30 Tinggi, Mutant V12T, Mutant Mayangsari and Mutant Lakatesan) and two commercial controls (Inpari 33 and Inpari 30 Ciherang Sub 1); the second factor comprised the three cropping sequences (R-R-R, M-M-R and V-V-R). Seedlings were transplanted 21 days after sowing into 3×4 m plots at 25×25 cm spacing, with one seedling per hill. Three random plants per plot, excluding border rows, were selected for monitoring. Preceding crop residues were incorporated naturally during primary tillage to a depth of 20 cm without external alteration. Fertilization followed the protocols of the Indonesian Center for Rice Research (ICRR).

Growth metrics comprised plant height (2, 4, 6 and 8 weeks after planting, WAP), vegetative tiller number (4 and 8 WAP), leaf surface area determined gravimetrically (4 and 8 WAP) and the root-to-shoot ratio (4 and 8 WAP) obtained by destructive sampling and oven-drying at 70°C for 72 hours. Yield components, comprising productive tillers, panicle length, grain number per panicle, 1000-grain weight and harvest index, were evaluated at harvest. After verifying data normality and variance homogeneity, factorial ANOVA ($p < 0.05$) and post-hoc Tukey's HSD test ($p < 0.05$) were performed using SAS v9.4 (PROC MIXED). Interrelationships among variables were analyzed using Pearson correlations on standardized data and visualized as structured heatmaps in RStudio using the corplot, Gally and pheatmap packages.

RESULTS AND DISCUSSION

Growth parameters Cropping sequences significantly influenced rice vegetative growth, driving stage-specific $G \times E$ interactions. Effects were non-significant for leaf area (4 and 8 WAP) and the 4-WAP root-to-shoot ratio, but significant for the 4-WAP tiller number ($p = 0.0338$) and the 8-WAP root-to-shoot ratio ($p = 0.0109$) (Table 1). Plant height variations emerged at later stages; R-R-R was tallest at 6 WAP (92.65 cm), but M-M-R became superior at 8 WAP (98.47 cm) relative to R-R-R (89.34 cm) and V-V-R (90.92 cm) (Table 2). This late-stage vigor under M-M-R was further supported by the maximum 8-WAP leaf surface area (2054.70 cm²) and vegetative tiller count (33.06), triggered by enhanced early below-ground biomass allocation (4-WAP root-to-shoot ratio of 0.72 versus 0.41 under R-R-R).

This phenotypic shift is likely associated with the transition from anaerobic lowland rice to aerobic maize cultivation, which is reported to disrupt the subsurface plow pan typical of intensive monocultures and thereby enhance nutrient availability. Incorporating high-N-demand maize

may further alter N and P dynamics through residual nutrient transfer from crop biomass (Duchene *et al.*, 2017) and the water regime of the preceding crop can modify the performance of the succeeding crop (Wei *et al.*, 2023). Although below-ground biochemical pathways were not quantified here, previous work indicates that such rotations recruit specialized microbial consortia (Guo *et al.*, 2024; Sujinah *et al.*, 2020; Zou *et al.*, 2023) that augment ammonification and dissimilatory nitrate reduction to ammonium, which could explain the enhanced N recycling efficiency (Wang *et al.*, 2023).

Rice genotypes exhibited significant phenotypic variability across vegetative traits. Plant height showed a significant $G \times E$ interaction only at 4 WAP, while responses at 2, 6 and 8 WAP were governed by main effects (Table 2). Mutant Lakatesan achieved the maximum height (105.64 cm), followed by GM 2 (104.29 cm) and Mutant Mayangsari (104.03 cm), although M-M-R consistently promoted greater overall growth vigor. Mutant Rojolele 30 Tinggi and Mutant Rojolele 30 Pendek maximized leaf expansion (up to 2294.90 cm²), whereas Inpari 33 produced the highest vegetative tiller count. The root-to-shoot ratio showed a significant $G \times E$ interaction at 8 WAP ($p = 0.0109$), indicating genotype-specific dry-matter partitioning strategies. Pearson correlation analysis confirmed this vegetative synergy, revealing a strong positive coupling ($r = 0.69$) between the 4-WAP tiller number and leaf area (Fig 1).

Yield components in diversified crop rotations, along with their respective soil baselines, significantly enhanced rice yield traits compared with continuous monoculture. Unlike vegetative parameters, yield components and the harvest index (HI) exhibited highly significant $G \times E$ interactions, specifically for grain number per panicle ($p = 0.0038$) and HI ($p < 0.0001$), confirming that biomass conversion efficiency depends heavily on the genetic-environmental interplay. Conversely, $G \times E$ interactions for 1000-grain weight ($p = 0.0723$) and panicle length ($p = 0.1853$) were non-significant, indicating that these traits were predominantly governed by genetic main effects

($p < 0.0001$; Table 1). Specific genotypes should therefore be deployed in tailored rotation systems to maximize responsive traits such as grain number, while stable components such as grain weight are best improved through genetic selection. Within this framework, the M-M-R sequence produced the most productive tillers (18.51) and the longest panicles (25.45 cm) relative to the R-R-R control (15.14 and 23.53 cm, respectively; Table 3). This reproductive superiority is likely optimised by the specific soil nutrient profile of the M-M-R legacy, particularly its higher baseline phosphorus availability, which potentially facilitates efficient cellular energy transfer during early panicle initiation (Wang *et al.*, 2021).

The highly significant $G \times E$ interaction for HI demonstrates that biomass conversion efficiency is dynamically modulated by cropping sequences and soil baselines (Fig 2). This modulation is potentially supported by distinct baseline soil nutrient profiles, such as the elevated phosphorus in the M-M-R system and the higher nitrogen in the V-V-R sequence, which may optimize resource translocation to reproductive sinks in line with nutrient-efficient ideotypes (Wijayanti *et al.*, 2023). Accordingly, the M-M-R (0.34) and V-V-R (0.35) sequences achieved substantially higher HI values than the R-R-R monoculture (0.22), confirming that diversified rotational matrices favor efficient economic dry-matter partitioning. Conversely, the depressed HI under R-R-R is associated with systemic deterioration in soil quality under continuous anaerobic cropping (Yang *et al.*, 2024), exacerbated by microbial nutrient immobilization under high C:N substrates from prolonged straw return (Xie *et al.*, 2022), compromised porosity (Yi *et al.*, 2020) and restricted macronutrient accessibility (Sun *et al.*, 2021). Although soil biochemical pathways were not quantified here, the literature attributes such agronomic shifts to recalibrated microbial functional pathways and optimized soil physicochemical properties (Wu *et al.*, 2025) and shows that crop establishment and nutrient management within a rotation measurably alter the physiological basis of rice yield formation (Bhangare *et al.*, 2025).

Table 1: ANOVA summary of the observed growth and yield variables.

Variables	Genotype (G)	Crop rotation sequences (E)	$G \times E$
Grain number per panicle	<0.0001**	<0.0001**	0.0038**
1000-grain weight	<0.0001**	0.7823ns	0.0723ns
Harvest index	<0.0001**	<0.0001**	<0.0001**
Leaf area (4 WAP)	0.0075**	<0.0001**	0.7137ns
Leaf area (8 WAP)	0.6908ns	0.1060ns	0.8190ns
Number of tillers (4 WAP)	0.0767ns	<0.0001**	0.0338*
Number of tillers (8 WAP)	0.0112*	0.0448*	0.7421ns
Root-shoot ratio (4 WAP)	0.1353ns	0.0002**	0.6019ns
Root-shoot ratio (8 WAP)	0.0360*	0.6274ns	0.0109*
Number of productive tillers	0.0127*	<0.0001**	0.0229**
Panicle length	0.0011**	0.0031**	0.1853ns

Note: Values represent p-values ($Pr > F$); ns= Not significant; WAP= Weeks after planting.

Table 2: Plant height at 2, 4, 6 and 8 weeks after planting, leaf surface area, number of vegetative tillers and root shoot ratio at 6 and 8 weeks after planting (WAP) of 12 rice genotypes.

Factors	Plant height			Area (cm ²) leaf surface			Number of vegetative tillers			Root shoot ratio	
	2 WAP	4 WAP	6 WAP	8 WAP	4 WAP	8 WAP	4 WAP	8 WAP	4 WAP	8 WAP	8 WAP
Crop rotation sequences											
Rice-rice-rice (R-R-R)	29.94a	53.99a	92.65b	89.34b	401.63a	1618.10a	16.36a	29.36a	0.41b	0.37a	
Maize-Maize-rice (M-M-R)	31.36a	55.18a	78.63a	98.47a	465.80a	2054.70a	19.56a	33.06a	0.72a	0.36a	
Vegetable-Vegetable-Rice (V-V-R)	29.49a	50.86a	78.99a	90.92b	301.63a	1972.30a	15.08a	29.97a	0.56ab	0.34a	
Genotypes											
V11	29.98bcd	53.16bc	78.91ab	93.41abc	378.56ab	1948.10a	17.67ab	30.00ab	0.62a	0.32a	
GM 28	30.22abc	55.51ab	83.60a	90.12bc	390.86ab	1494.80a	16.78ab	24.78b	0.83a	0.29a	
GM 2	31.35abc	57.52a	83.56a	104.29ab	363.75ab	1902.80a	13.33b	27.89ab	0.56a	0.34a	
GM 8	32.87a	53.84abc	73.55bcd	80.21c	425.39ab	1712.20a	18.89ab	31.11ab	0.48a	0.33a	
Mutant lampung kuning	29.01cd	50.76cd	73.49bcd	90.61bc	405.90ab	1569.30a	16.78ab	29.11ab	0.41a	0.38a	
Mutant rojolele 30 pendek	29.14cd	50.87cd	75.64bc	97.62ab	327.54ab	2253.20a	16.33ab	35.67a	0.55a	0.41a	
Mutant rojolele 30 tinggi	29.44cd	51.85bcd	76.44abc	92.43abc	353.44ab	2294.90a	17.56ab	35.00ab	0.78a	0.44a	
Mutant V12T	30.45abc	51.88bcd	78.04ab	97.20ab	332.49ab	1750.10a	18.11ab	32.33ab	0.52a	0.39a	
Mutant mayangsari	32.32ab	57.58a	80.67ab	104.03ab	450.97ab	2047.40a	16.56ab	26.22ab	0.59a	0.34a	
Mutant lakatesan	31.58abc	57.51a	80.11ab	105.64a	445.37ab	1569.30a	16.33ab	31.22ab	0.57a	0.29a	
Inpari 33	29.40bcd	50.74cd	70.60cd	80.47c	489.94a	1904.90a	20.22a	35.11ab	0.44a	0.35a	
Inpari 30 ciharang Sub 1	27.32d	48.94d	66.46d	78.90c	312.23b	2098.50a	15.44ab	31.11ab	0.47a	0.39a	
Average	30.26	53.35	76.76	92.81	389.70	1881.72	17.00	30.80	0.57	0.36	
Interaction	(-)	(+)	(-)	(-)	(-)	(-)	(+)	(-)	(-)	(+)	

Note: Values in the same column followed by the same letter are not significantly different ($p < 0.05$) based on Tukey's honestly significant difference (HSD) test. (-) denotes no significant interaction; (+) denotes significant interaction.

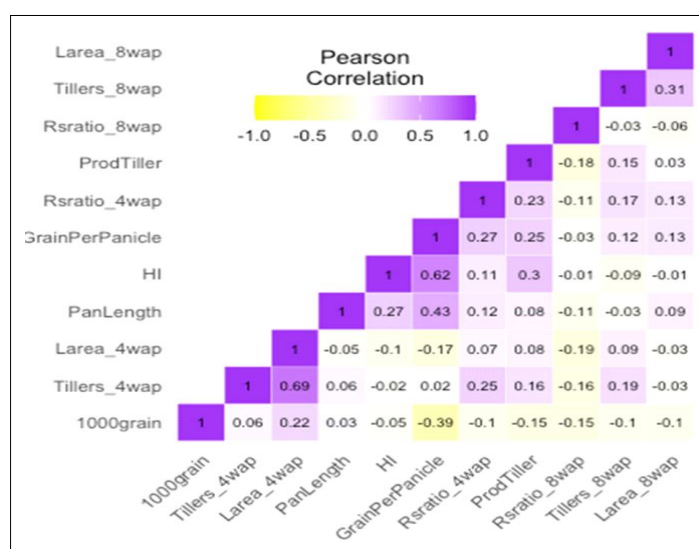


Fig 1: Heat map of correlations among the observed variables.

Table 3: Number of productive tillers and panicle length of 12 rice genotypes.

Factors	Number of productive tillers	Panicle length (cm)
Crop rotation sequences		
R-R-R	15.14c	23.53b
M-M-R	18.51a	25.45a
V-V-R	16.94b	24.96ab
Genotypes		
V11	17.52ab	23.77ab
GM 28	16.63ab	26.56a
GM 2	15.59ab	25.21a
GM 8	16.55ab	24.89a
Mutant lampung kuning	15.98ab	24.63a
Mutant rojolele 30 pendek	17.56ab	24.35ab
Mutant rojolele 30 tinggi	16.81ab	25.55a
Mutant V12T	18.46a	24.63a
Mutant mayangsari	17.29ab	25.77a
Mutant lakatesan	18.65a	20.69b
Inpari 33	16.83ab	25.09a
Inpari 30 ciherang Sub 1	14.48b	24.35ab
Average	16.86	24.64
Interaction	(+)	(-)

Note: Values in the same column followed by the same letter are not significantly different ($P < 0.05$) based on Tukey's honestly significant difference (HSD) test. (-) denotes no significant interaction; (+) denotes significant interaction.

HI correlated strongly with grain number per panicle ($r = 0.62$) and moderately with productive tillers ($r = 0.30$), identifying both as vital determinants of biomass partitioning. Conversely, an inverse physiological trade-off occurred between 1000-grain weight and grain number per panicle ($r = -0.39$). Ontogenetic resource reallocation

from vegetative growth to reproductive structures was evidenced by a decaying correlation between leaf area and tiller number from 4 WAP ($r = 0.69$) to 8 WAP ($r = 0.31$; Fig 1). Grain number per panicle, therefore, serves as a reliable indirect selection criterion for high harvest efficiency in non-monoculture matrices. To circumvent the sink-capacity limitation imposed by the grain number-grain weight trade-off, breeding programs must prioritize genotypes able to maintain high grain-filling rates under the dynamic nutrient fluxes of M-M-R and V-V-R.

Pronounced $G \times E$ interactions predominantly governed reproductive traits such as grain number per panicle and HI. GM 8 exhibited high phenotypic plasticity, maximizing yield potential with 299.33 grains per panicle under M-M-R compared with 137.00 under R-R-R monoculture (Fig 3). Similarly, Mutant Mayangsari doubled its grain count when moving from R-R-R (111.00) to the diversified sequences (206.67-215.33). Overall, GM 8 (227.00), Mutant Rojolele 30 Tinggi (217.11) and Mutant V12T (215.67) maximized grain counts, whereas Mutant Lakatesan and the Inpari lines consistently underperformed. For 1000-grain weight, GM 8 remained superior and stable across all environments (30.69 g), followed by Inpari 33 (27.85 g) and Inpari 30 Ciherang Sub 1 (26.42 g), all significantly outperforming low-weight mutants such as Mutant V12T (15.65 g) and Mutant Rojolele 30 Pendek (15.85 g) (Fig 4).

The present study establishes how specific rotational soil legacies govern grain development and harvest efficiency, an issue central to the development of climate-resilient genotypes for degraded tropical soils. GM 8 demonstrated peak partitioning efficiency with a maximum HI of 0.51 under V-V-R, whereas Inpari 30 Ciherang Sub 1 recorded the lowest efficiency (HI = 0.17) within the degraded R-R-R matrix. While intrinsic genetic potential establishes performance baselines, transitioning from intensive monoculture to maize or vegetable-based

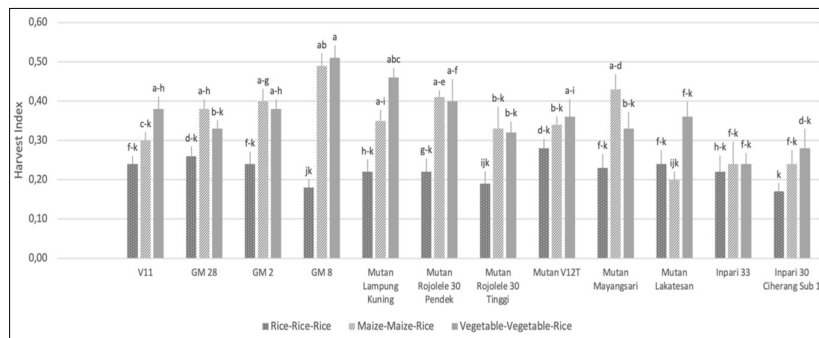


Fig 2: Harvest index of 12 rice genotypes.

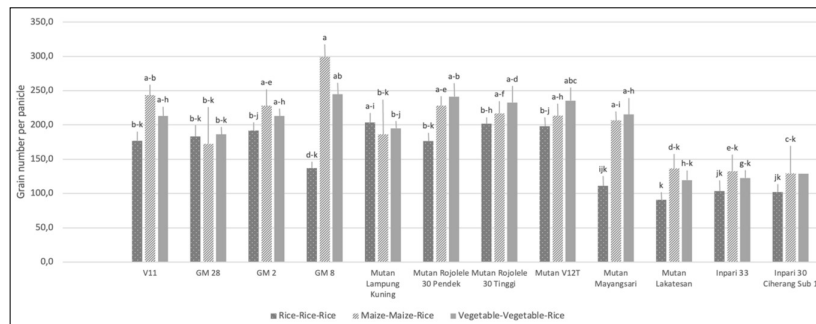


Fig 3: Grain number per panicle of 12 rice genotypes.

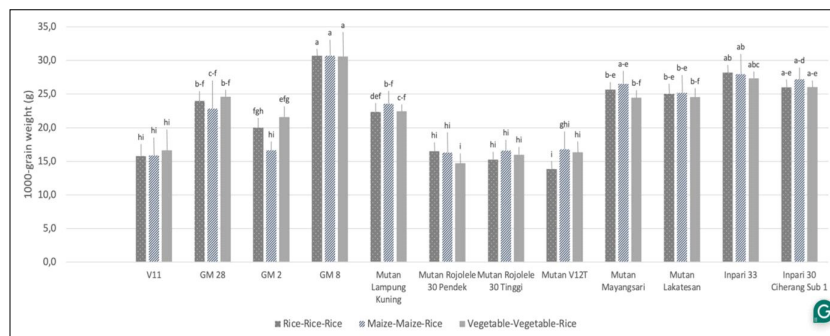


Fig 4: 1000-grain weight of 12 rice genotypes.

rotations provides the edaphic framework required to optimize the conversion of dry matter into grain yield.

CONCLUSION

Diversified crop rotation sequences, namely maize-maize-rice (M-M-R) and vegetable-vegetable-rice (V-V-R), significantly influenced both the vegetative development and the reproductive yield attributes of rice. The M-M-R sequence systematically enhanced vegetative vigor and yield components, as evidenced by increased plant height, greater tiller abundance and elevated grain counts per panicle. Diversified rotations also led to a significantly higher harvest index; V-V-R and M-M-R achieved HI values of 0.35 and 0.34, respectively, compared with 0.22 under continuous R-R-R monoculture. Among the assessed

genotypes, GM 8 showed the greatest phenotypic plasticity, achieving optimal harvest efficiency within the vegetable-based environment. Candidate genotypes under non-monoculture frameworks should therefore be evaluated not only for crude yield potential but also for HI plasticity. Because these insights derive from a single rotation cycle, continuous multi-cycle monitoring is warranted to validate the long-term sustainability and cumulative soil-enrichment benefits of these rotational systems.

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Disclaimers

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Informed consent

Not applicable. This study did not involve human participants or animal subjects. The plant materials used in this study complied with relevant institutional, national and international guidelines and legislation.

Conflict of interest

The authors declare that there are no conflicts of interest regarding the publication of this article. The funder had no role in the design of the study, the collection or analysis of data, the decision to publish, or the preparation of the manuscript.

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