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GENETIC VARIABILITY AND MORPHOLOGICAL ADAPTATION CONFERRING FLOODING TOLERANCE IN MUNG BEAN (*VIGNA RADIATA* L.)

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SUMMARY

In mung bean (*Vigna radiata* L. Wilczek), flooding is a major abiotic constraint limiting productivity in flood-prone areas. The presented study aimed to evaluate the morpho-agronomic traits of 15 mung bean genotypes under waterlogging for zero, seven, and 10 days in a randomized complete design with factorial arrangement and three replications. Analysis of variance revealed significant effects of genotypes, flooding durations, and their interactions on the pod number, seed weight, trifoliate leaves, and root traits. After seven days of flooding, genotypes Murai and Lokal Majenang produced the highest pod number (10.33 and 7.00 pods, respectively), while genotypes Kasu and Kutilang produced the fewest pods (5.33 and 8.00 pods, respectively) after 10 days of flooding. Root traits were highly sensitive, particularly with genotypes Kasu and Kutilang expressing better root length (14.1 and 18.0 cm, respectively) and root weight (1.9 and 2.6 g, respectively) under flooding stress conditions. Broad-sense heritability was moderate for root length (31.7%) and wet root weight (22.0%), whereas seed and stover traits showed low heritability. Pod number and root length emerged as key indicators of flooding tolerance. Genotypes Kasu, Lokal Majenang, and Kutilang were the recommended promising donors for breeding waterlogging-tolerant mung beans.

Keywords: Mung bean (*V. radiata* L.), flooding stress, heritability, landraces, yield traits

Key findings: Flooding stress conditions significantly affected and reduced the growth and yield traits in mung bean (*V. radiata* L.), and the accessions showed different responses, revealing considerable genetic variability. Pod number and root length surfaced to be the most sensitive and reliable traits for screening tolerance in mung beans.

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INTRODUCTION

With climate change, flooding and waterlogging are the crucial abiotic stress factors affecting legume production, leading to reduced photosynthesis and nutrient uptake and, eventually, considerable yield losses (Wu and Yang, 2016; Pan *et al*., 2021). Globally, waterlogging can reduce legume yields by 20%–50%, depending on stress duration and soil conditions (Sen-Gupta *et al*., 2023), underscoring its significant impact on productivity in flood-prone areas. Mung bean (*Vigna radiata* L. Wilczek) is a short-duration pulse crop with high nutritional and economic value, widely grown in Asia and adapted to diverse cropping systems (Pataczek *et al*., 2018; Kumar *et al*., 2022). Despite its agronomic advantages, the mung bean remains relatively unexplored for tolerance to flooding stress conditions compared with other legumes. Under root hypoxia, mitochondrial respiration desists, ATP production declines, and reactive oxygen species accumulate, impairing nutrient transport and destabilizing plant growth (Ma *et al*., 2022). These physiological disruptions form the basis for adaptive responses, such as aerenchyma development, adventitious root formation, and enhanced root plasticity under flooding.

Physiological studies have revealed legume tolerance to waterlogging involves adaptive mechanisms, such as adventitious root formation, aerenchyma development, and antioxidative enzyme activities (Raina *et al*., 2019; Men *et al*., 2020). However, scarce information exists on the genetic variability of mung bean genotypes in relation to flooding tolerance. Identifying genetic variability and heritable traits is essential in breeding programs aiming to improve resilience to waterlogging, as genetic diversity provides the foundation for selecting adaptive traits under hypoxic environments (Manavalan *et al*., 2009). Previous reports emphasized the importance of yield-related and root traits of mung beans and other legumes for adaptation to abiotic stress conditions (Hoyos-Villegas *et al*., 2017; Ikram *et al*., 2022). However, systematic evaluation of local landraces and farmer cultivars of mung bean under controlled flooding remains limited, particularly in Indonesia, where mung bean is the major food and export crop.

Genetic improvement in mung beans for abiotic stress tolerance lags compared with cereals and other major legumes, partly due to a narrow genetic basis and limited investment in its breeding programs (Nair *et al*., 2019). This situation necessitates expanding the phenotypic screening in stress environments to capture genetic variability in the landraces, which often harbor overlooked adaptive traits in modern cultivars.

Flood-related stress in legumes often interacts with other constraints, such as nutrient deficiency and pest susceptibility, exacerbating yield instability under the smallholding systems of the farming community (Pan *et al*., 2021). These complex stress interactions emphasize that developing tolerant mung bean cultivars would enhance crop stability with sustainable production and also improve food security in climate-vulnerable regions. The advances in genomics and phenomics provide opportunities to dissect tolerance mechanisms more effectively, and combining morpho-agronomic evaluation with molecular breeding tools is considerably notable as a strategic pathway for improvement in mung beans. However, this type of concrete progress crucially depends on the robust baseline data from multi-genotype evaluations under controlled stress environments (Somta *et al*., 2022).

Furthermore, with increasing climate change and its uncertainties, renewed interest emerges in exploring the plants' root system architecture and physiological plasticity as critical components for stress resilience (Liu *et al*., 2021). Integrating such knowledge with conventional and molecular breeding approaches could accelerate the development of waterlogging-tolerant mung beans. However, empirical data on genetic variability under controlled flooding conditions, especially from Southeast Asian germplasm, remain scarce. In this study, 15 mung bean landraces, consisting of local farmer cultivars collected from multiple regions of Indonesia, were

Table 1. Mung bean accessions used in this study.

No.	Code	Local name	Site of origin
1	G-1	Lokal Belu	East Nusa Tenggara
2	G-2	Lokal Jerowaru	West Nusa Tenggara
3	G-3	Tecer Hitam	Balitkabi Malang, East Java
4	G-4	Lok. Silu-Pol-Hit	North Sulawesi
5	G-5	Murai	Balitkabi Malang, East Java
6	G-6	Kasu	North Sulawesi
7	G-7	Kah A	North Sulawesi
8	G-8	Lepe	North Sulawesi
9	G-9	Lokal Wulanggitan-2	East Nusa Tenggara
10	G-10	Lokal Bajawa Ngada	East Nusa Tenggara
11	G-11	Uwi Kayu	East Nusa Tenggara
12	G-12	Ue	East Nusa Tenggara
13	G-13	Perkutut	Balitkabi Malang, East Java
14	G-14	Lokal Majenang B	Southeast Sulawesi
15	G-15	Kutilang	Balitkabi Malang, East Java

options to represent genetic diversity from flood-prone agroecological zones. Therefore, the subsequent study aimed to a) assess the morpho-agronomic responses of 15 mung bean landraces under different flooding durations, b) estimate genetic variability and heritability in the key traits, and c) identify the promising genotypes for developing waterlogging-tolerant mung beans through breeding.

MATERIALS AND METHODS

Plant material and experimental design

Fifteen mung bean (*V. radiata* L. Wilczek) genotypes comprising farmer varieties and local landraces collected from different regions of Indonesia sustained evaluation under different flooding durations (Table 1). The experiment proceeded in the greenhouse of the Agency for Agricultural Assembly and Modernization–Biotechnology and Genetic Resources (BRMP–Biogen), Bogor, Indonesia. A randomized complete design (RCD) with a factorial arrangement commenced, consisting of two factors: mung bean genotypes and flooding durations (0, 7, and 10 days), each with three replications. Mung bean seeds underwent sowing in plastic buckets (25 cm × 30 cm; approximately 15 L volume), maintaining two plants per bucket after thinning. Fertilization used the NPK compound fertilizer (15-15-15) at 100 kg ha^{-1} equivalent (≈1.5 g per bucket) 20 days after sowing, followed by manual weeding at the same interval to minimize weed competition.

Flooding treatments

Flooding induction occurred 14 days after planting, with 5 cm of standing water maintained above the soil surface for seven and 10 days. Water-level monitoring occurred daily, replenishing manually with tap water to consistently maintain a depth of 5 cm throughout the flooding period. After treating the mung bean plants for the specified duration, draining the water followed, with regular watering resumed until harvest. Control plants (with zero days of flooding) remained under normal watering conditions, with approximately 500–700 mL of water applied per bucket per day to keep the soil near field capacity without surface flooding.

Trait measurement

The data recorded on seven morpho-agronomic traits continued in the mung bean genotypes, including pod number and weight, seed weight, trifoliate leaf number, stover weight, and root length and weight. These traits were the selected indicators of yield performance and

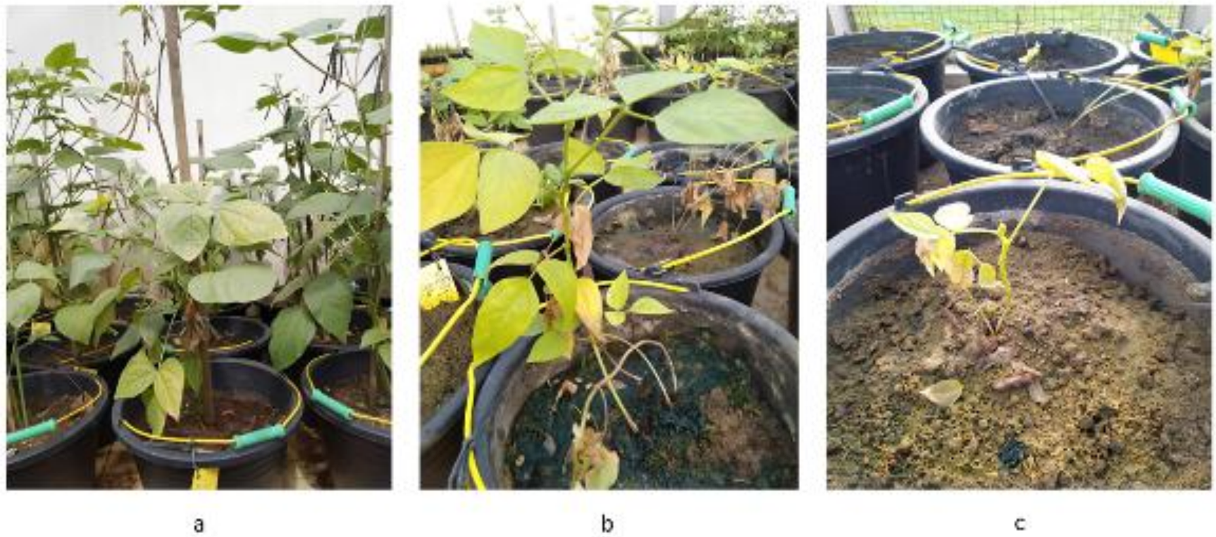

Figure 1. The traits of mung bean genotype plants experiencing flood stress. Depicted the plants at the a) day 0 (control-before flooding), b) day 7 after flooding (moderate-stress symptoms), and c) day 10 after flooding (severe-stress symptoms). This development demonstrates the worsening impact of flooding on plant growth, leaf pigmentation, and the general physiological wellbeing of mung beans.

stress adaptation, following previous evidence that they are responsive to waterlogging stress and can discriminate tolerant from susceptible genotypes (Ikram *et al*., 2022). Furthermore, their combined evaluation provides a holistic assessment of plant performance in stress conditions, which is essential for identifying tolerant genotypes.

Statistical analysis

Multivariate analysis of variance (MANOVA) succeeded in evaluating the effects of mung bean genotypes, flooding durations, and their interactions on all the studied traits. The factors showing significance for various traits entailed further analysis using the univariate analysis of variance (ANOVA). Means comparison and separation took place using the least significant difference (LSD) test at the 5% probability level. Genotypic and phenotypic variances and broad-sense heritability (H^2) values for various traits incurred estimations (Allard, 1999).

RESULTS

Plants' response to flooding

The flooding stress conditions reduced the mung bean (*Vigna radiata* L. Wilczek) genotype plants' vigor. Within a few days of waterlogging, visible stress symptoms appeared, including slower shoot elongation, reduced leaf expansion, and progressive yellowing compared with the control plants. After 10 days of continuous flooding, several mung bean plants collapsed and eventually died, while the plants in the control treatment remained green and showed normal growth (Figure 1). Substantial genotypic variation was evident. Some plants ceased producing new shoots and displayed severe injury, whereas others could maintain limited growth. Notably, a few mung bean genotypes could still flower and set pods despite flooding, indicating differential tolerance levels within the tested population. These observations emphasized the presence of a wide phenotypic diversity under

Table 2. Multivariate analysis of variance (MANOVA) for the effects of genotypes, flooding durations, and their interactions.

Effect	Test Statistic	Value	Num DF	Den DF	F-value	Significance
Intercept	Wilks' λ	0.4932	8	83	10.66	***
	Pillai's trace	0.5068	8	83	10.66	***
	Hotelling–Lawley	1.0277	8	83	10.66	***
	Roy's root	1.0277	8	83	10.66	***
Genotype	Wilks' λ	0.0341	112	593.66	3.28	***
	Pillai's trace	2.4616	112	720	2.86	***
	Hotelling–Lawley	4.9965	112	377.54	3.63	***
	Roy's root	1.9776	14	90	12.71	***
Flooding	Wilks' λ	0.5627	16	166	3.46	***
	Pillai's trace	0.4586	16	168	3.12	***
	Hotelling–Lawley	0.7392	16	132.28	3.80	***
	Roy's root	0.6838	8	84	7.18	***
Genotype × Flooding	Wilks' λ	0.0366	224	656.61	1.57	***
	Pillai's trace	2.4787	224	720	1.44	***
	Hotelling–Lawley	4.6764	224	458.24	1.70	***
	Roy's root	1.5363	28	90	4.94	***

Significance levels – ***p* < 0.001*; p* < 0.01*; p* < 0.05*;* ns = not significant. All effects tested were highly significant ().

Table 3. Analysis of variance of the effects of genotypes, flooding durations, and their interactions on plant traits.

Source of Variation	df	PN	WPW	DSW	TN	WSW	DSWt	RL	WRW
Corrected Model	46	6.93***	4.87***	6.52***	5.37***	2.07**	1.69*	5.28***	3.86***
Intercept	1	186.10***	137.90***	183.64***	177.29***	71.10***	52.58***	271.55***	161.34***
Genotype	14	3.75***	2.57**	3.34***	3.78***	1.62ns	1.23ns	5.91***	3.76***
Flooding	2	96.07***	71.57***	92.72***	67.73***	24.36***	18.75***	45.58***	34.03***
Genotype × Flooding	28	2.61***	1.52ns	2.33**	1.98**	0.75ns	0.77ns	2.42**	2.04**
Replication	2	0.41ns	1.17ns	1.18ns	1.67ns	1.36ns	0.74ns	0.65ns	0.02ns
Residual	88	–	–	–	–	–	–	–	–

Values are F-statistics; significance levels – ****p* < 0.001; ***p* < 0.01; *p* < 0.05; ns = not significant. Trait codes – PN: pod number; WPW: wet pod weight; DSW: dry seed weight; TN: trifoliate number; WSW: wet stover weight; DSWt: dry stover weight; RL: root length; and WRW: wet root weight.

flooding stress conditions. Among the tested genotypes, G-6 and G-15 consistently maintained pod set and growth under flood stress, while G-5 showed pronounced susceptibility and severe damage. This contrast provides a clear and practical basis for distinguishing tolerant and susceptible mung bean genotypes.

Genotype by flooding effects

Multivariate and univariate analyses enunciated significant (p ≤ 0.01) effects of the mung bean genotypes, flooding durations, and their interaction for pod number, seed weight, trifoliate leaves, root length, and root weight (Tables 2 and 3). The genotypes' differences were most evident for reproductive and root traits. Some mung bean genotypes could maintain pod production and root development under flooding conditions, whereas others showed severe reductions in growth and development. Although the MANOVA/ANOVA results clearly indicate differential responses, the identification of specific tolerant and sensitive genotypes, along with their comparative trait values, is available in the subsequent section. In contrast, flooding durations alone mainly influenced the stover traits. The nonsignificant genotype-flooding interaction indicates growth suppression was generally uniform across all mung bean genotypes. These findings suggest reproductive and below-ground traits are more informative than vegetative traits for distinguishing stress-tolerant landraces under flooding.

Morphological responses

Under both flooding durations, the morphological responses revealed consistent decline across most mung bean genotypes (Table 4). The traits trifoliate number (TN), root length (RL), root weight (WRW), and dry shoot weight (DSWt) received significant effects with a reduction from prolonged flooding in the mung bean genotypes. With 10 days of flooding, nearly all genotypes (12 of 15) exhibited near-total inhibition of root traits; only genotypes G-6, G-8, and G-15 retained measurable root length and wet root weight at 10 days. However, the genotypes G-6 and G-15 consistently retained relatively longer roots and higher root biomass across treatments. At the same time, G-8 demonstrated partial retention at 10 days, and G-14 retained root traits at seven days but not at 10 days. These contrasting patterns were also evident in the heatmap (Figure 2b): darker shades denote higher RL and WRW, with tolerant genotypes (G-6, G-8, G-15) appearing as darker blocks at 10 days, whereas most genotypes display lighter shades, indicating severe reduction. These results are consistent with physiological indices that highlighted root vigor and photosynthetic retention as robust predictors of flooding tolerance (Ikram *et al*., 2022). The maintained root growth under flooding stress conditions in these mung bean genotypes supports their potential role as promising parental genotypes for future breeding programs.

Yield-related responses

Flooding stress conditions markedly affected and eventually reduced the yield-related traits in mung bean genotypes (Table 5). Pod number (PN) with 18–29 pods under control declined to fewer than 12 pods with seven days of flooding in most mung bean genotypes, and nearly zero pod numbers were visible with 10 days of flooding. Only the genotypes G-5 and G-14 maintained more than 10 pods with seven days of flooding, while G-15 and G-6 even produced pods with 10 days of flooding, albeit at reduced levels. Dry seed weight (DSW) followed a similar trend, and the mung bean genotypes G-6 and G-15 retained 5.8 and 6.1 g plant^{-1}, respectively, compared with less than 3 g plant^{-1} in the other genotypes. These variations highlighted the considerable sensitivity of mung bean reproductive traits to flooding, with the same also having been previously reported in the mung bean genotypes (Haeften *et al*., 2023). The heatmap visualization (Figure 2a) showed distinct clustering patterns: tolerant genotypes (G-6, G-15, and G-14) were indicative of warmer shades corresponding to higher PN and DSW values, whereas sensitive genotypes (G-2, G-3, G-7, and G-10) appeared in more fabulous shades, indicating drastic yield reductions. The consistency of these results with earlier findings reinforces the importance of reproductive resilience as a key target for selection under waterlogging stress conditions.

Genetic variability and heritability

The variance component analysis revealed moderate-to-high heritability for several key traits, including pod number (PN), dry seed weight (DSW), root length (RL), and wet root weight (WRW) (Table 6). These results authenticated genotypic variations significantly contribute to the observed responses, and these traits were amenable to selection in future breeding programs. Mean-square analysis indicated significant genotypic variations for pod number, trifoliate leaves, root length, and root weight, while stover traits showed nonsignificant genetic effects. Broad-sense heritability values were moderate for RL (31.7%) and WRW (22.0%), suggesting genetic influence and potential for further selection. However, the seed weight and stover traits had low heritability (<20%), implying considerable environmental effects (Table 6).

Table 4. Effect of flooding durations on morphological traits across 15 mung bean genotypes.

Genotype	TN 0-days	TN 7-days	TN 10-days	RL 0-days	RL 7-days	RL 10-days	WRW 0-days	WRW 7-days	WRW 10-days	DSWt 0-days	DSWt 7-days	DSWt 10-days
G-1	13.00	1.33	0.00	11.61	8.00	0.00	4.02	0.81	0.00	11.90	1.75	0.00
G-2	12.00	0.00	0.00	15.33	0.00	0.00	3.18	0.00	0.00	9.23	0.00	0.00
G-3	8.00	0.00	0.00	12.94	4.00	0.00	3.22	0.73	0.00	7.07	0.00	0.00
G-4	12.33	4.67	0.00	10.83	3.92	0.00	3.33	1.70	0.00	14.27	16.46	0.00
G-5	12.67	4.33	0.00	13.83	12.58	0.00	2.24	2.64	0.00	9.83	7.01	0.00
G-6	9.00	4.67	4.67	14.17	10.50	14.11	4.02	1.77	1.89	9.31	6.61	3.10
G-7	5.33	2.67	0.00	13.17	6.00	0.00	0.87	1.37	0.00	4.03	2.53	0.00
G-8	1.33	0.00	0.00	4.83	0.00	7.72	0.44	0.00	0.52	3.32	0.00	0.00
G-9	8.67	1.67	0.00	15.56	5.67	0.00	3.40	0.66	0.00	14.96	0.80	0.00
G-10	3.67	0.00	0.00	9.06	0.00	0.00	2.03	0.00	0.00	14.44	0.00	0.00
G-11	5.67	0.00	0.00	13.83	0.00	0.00	1.51	0.00	0.00	8.36	0.00	0.00
G-12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
G-13	12.33	4.33	0.00	17.69	14.00	0.00	2.76	1.66	0.00	11.26	3.72	0.00
G-14	6.00	6.00	0.00	20.00	15.11	0.00	2.93	4.47	0.00	8.37	4.77	0.00
G-15	8.33	3.33	4.67	16.33	11.83	18.00	2.32	2.12	2.61	6.05	1.74	4.59

LSD (α = 0.05) for traits in this table: TN: 5.09; RL: 8.12; WRW: 1.93; DSWt: 10.68.
Trait codes – TN: trifoliate number; WSW: wet stover weight; DSWt: dry stover weight; RL: root length; and WRW: wet root weight.

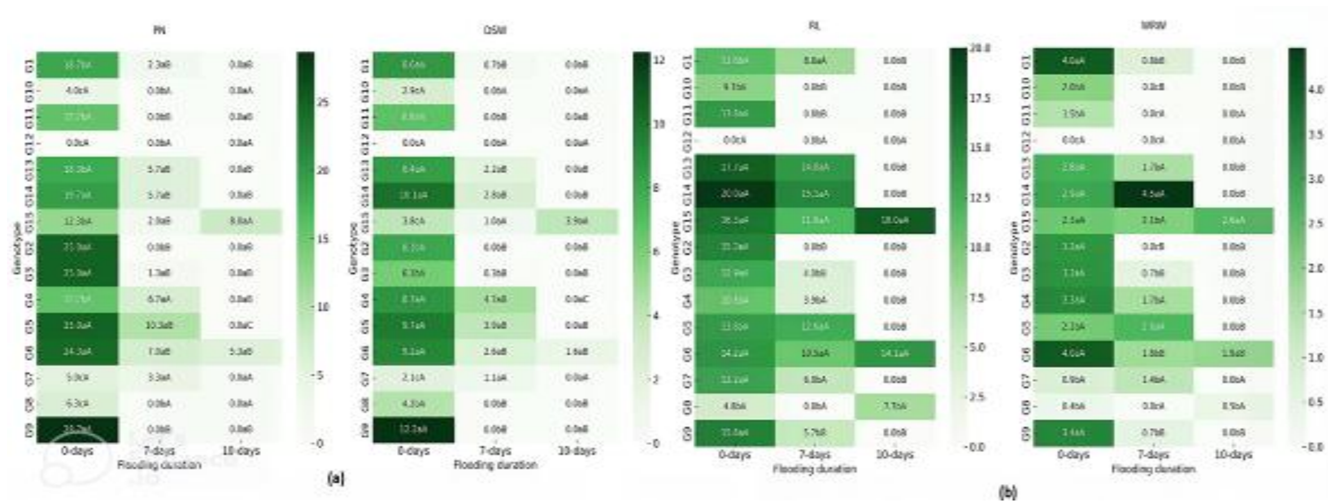

Figure 2. Heatmaps of yield and root traits in 15 mung bean genotypes under 0, 7, and 10 days of flooding. a) Pod number (PN) and dry seed weight (DSW), b) Root length (RL) and root weight (WRW). Letters denote significant differences (LSD, α = 0.05).

Table 5. Effect of flooding durations on yield traits across 15 mung bean genotypes.

Genotype	PN 0-days	PN 7-days	PN 10-days	WPW 0-days	WPW 7-days	WPW 10-days	DSW 0-days	DSW 7-days	DSW 10-days
G-1	18.67	2.33	0.00	12.28	1.06	0.00	8.56	0.71	0.00
G-2	25.00	0.00	0.00	10.25	0.00	0.00	8.06	0.00	0.00
G-3	25.00	1.33	0.00	8.47	0.41	0.00	6.14	0.28	0.00
G-4	15.67	6.67	0.00	11.81	7.75	0.00	8.69	4.75	0.00
G-5	25.00	10.33	0.00	14.10	4.64	0.00	9.71	3.86	0.00
G-6	24.33	7.00	5.33	12.90	3.99	2.43	9.22	2.63	1.57
G-7	5.00	3.33	0.00	3.01	1.34	0.00	2.11	1.1	0.00
G-8	6.33	0.00	0.00	6.21	0.00	0.00	4.25	0.00	0.00
G-9	28.67	0.00	0.00	16.25	0.00	0.00	12.24	0.00	0.00
G-10	4.00	0.00	0.00	3.91	0.00	0.00	2.94	0.00	0.00
G-11	15.67	0.00	0.00	8.87	0.00	0.00	6.80	0.00	0.00
G-12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
G-13	18.33	5.67	0.00	11.10	2.97	0.00	8.35	2.25	0.00
G-14	19.67	5.67	0.00	12.06	3.48	0.00	10.06	2.79	0.00
G-15	12.33	2.00	8.00	7.57	0.94	3.82	3.83	1.03	3.85

Note: LSD (α = 0.05) for traits in this table: PN: 9.19; WPW: 6.13; DSW: 3.90. Trait codes – PN: pod number; WPW: wet pod weight; and DSW: dry seed weight.

Table 6. Variance components and heritability estimate of morpho-agronomic traits in mung bean genotypes under flooding stress.

Trait Code	Genotype MS	Flooding MS	G × F MS	Error MS	CV (%)	σ^2g	σ^2f	H^2 (%)	Category
PN	121.93*	3124.94*	85.01*	32.53	1.38	58.14	364.47	15.95	Low
WPW	36.61*	1019.28*	16.63	14.24	1.59	12.99	118.41	10.98	Low
DSW	19.18*	532.45*	6.79*	5.74	1.57	6.74	62.26	10.83	Low
TN	36.67*	657.43*	16.23*	9.71	1.70	14.40	78.90	18.25	Low
WSW	668.33	10059.71*	562.88	412.92	1.75	272.76	1197.30	22.78	Moderate
DSWt	53.48	817.99*	32.44	43.62	1.78	14.10	94.45	14.93	Low
RL	149.24*	1150.39*	16.31*	25.24	1.72	46.77	147.39	31.73	Moderate
WRW	5.45*	49.33*	0.02*	1.45	1.77	1.34	6.10	21.98	Moderate

MS = mean square; σ^2g = genotypic variance; σ^2f = phenotypic variance; H^2 = broad-sense heritability. Indicates significance at $p < 0.05$. Trait codes – PN: pod number; WPW: wet pod weight; DSW: dry seed weight; TN: trifoliate number; WSW: wet stover weight; DSWt: dry stover weight; RL: root length; WRW: and wet root weight. Categories: Low (<20%), Moderate (20%–50%).

Overall, the results exhibited the existence of exploitable genetic variability for flooding tolerance traits in mung bean genotypes, providing a substantial basis for genetic improvement through future breeding.

DISCUSSION

Flooding durations significantly affected and reduced the pod number and seed weight across most mung bean genotypes, confirming yield traits appeared highly susceptible to root-zone hypoxia (Fukao *et al*., 2019). However, three tolerant genotypes (G-6, G-14, and G-15) maintained partial productivity under prolonged flooding stress, reinforcing that tolerance remains relatively rare within mung bean germplasm. Contrastingly, the susceptible genotype G-5 showed severe yield reduction, emphasizing the broad spectrum of responses within the tested accessions. These observations were consistent, in particular, with observed findings during reproductive growth stages in mung beans (Haeften *et al*., 2023). The tolerant mung bean genotypes with superior performance likely carry adaptive alleles that buffer photosynthetic inhibition and assimilate loss even under flooding conditions (Loreti *et al*., 2016). Reports on comparable patterns have also surfaced, where hypoxia disproportionately affects the reproductive traits in other legumes. Moreover, recent reviews emphasize the reproductive stage is the most critical phase where flooding stress exerts yield loss, making reproductive resilience a key breeding target (Wiraguna *et al*., 2021).

Morphological responses in the tolerant genotypes further confirm this adaptive variation. Although flooding reduced root length and biomass, they retained higher values, indicating root growth under hypoxia as a key adaptive trait. Sustained root activity facilitates internal oxygen diffusion, nutrient uptake, and water balance, thus enhancing survival and enabling partial productivity in stress (Sauter, 2013). Tolerant mung bean lines also preserved more shoot biomass, enabling limited pod filling despite stress conditions. Ikram *et al*. (2022) reported physiological indices, such as excitation pressure and photosynthetic efficiency, predicted tolerance at the pod-filling stage, consistent with our findings on sustained root and shoot activity. Moreover, stomatal closure under flooding directly limits CO_2 uptake, reducing chloroplast carbon supply and photosynthesis (Camisón *et al*., 2020). Therefore, the various responses shown by mung bean landraces report the relevance through a general decrease in the number of leaves (trifoliate), stover weight, and pod formation.

In crop plants, the adaptation to hypoxic environments shows a frequent association with morphological variations, such as aerenchyma, which facilitate oxygen diffusion to submerged root tissues and reduce the severity of anoxia (Nurrahma *et al*., 2023). Moreover, aerenchyma reflects severe flooding stress conditions (Aslam *et al*., 2023). Beyond oxygen deprivation, flooding induces secondary stresses, such as reduced nutrient availability due to altered soil redox potential, decreased root activity, impaired nutrient absorption, and, ultimately, lowered biomass accumulation (Cao *et al*., 2022). These stress factors may limit nutrient uptake and assimilate translocation, and thus, further constrain yield in stress conditions. Under flooding conditions, nutrient-use efficiency has been experimentally demonstrated in lentils, where anatomical and biochemical responses, including osmotic adjustments and antioxidant defense, helped buffer stress (Bharadwaj *et al*., 2023). These findings suggested flooding tolerance arises from an integrated suite of morphological, physiological, and biochemical strategies, not solely by a single trait (Manghwar *et al*., 2024).

Physiological processes likely underpin the contrasting responses among the genotypes under flooding stress conditions. Tolerant mung bean types, such as G-6, G-14, and G-15, may deploy effective ethylene and ABA-mediated signaling that promotes adventitious root formation, aerenchyma development, and antioxidant defenses to mitigate the oxidative stress conditions. These results align with findings in legumes and cereals, where survival under waterlogging revealed linkages to regulated root initiation, antioxidant activation, and metabolic adjustments to sustain cellular energy (Fukao & Bailey-Serres, 2008; Kyu *et al*., 2021). Kyu (2024) further identified genomic loci as having an association with mung bean root plasticity and waterlogging tolerance. In rice, comparable evidence also highlighted hormonal crosstalk (ethylene–GA–ABA) in initiating adaptive root structures (Nishiuchi *et al*., 2012). Although the presented study did not directly assess the metabolic traits, the consistency of the tolerant mung bean suggests that efficient energy metabolism under hypoxia is a critical component of tolerance. In tolerant plants, hypoxia suppresses oxidative phosphorylation and forces a shift toward fermentative metabolism while maintaining ATP production and activating antioxidant systems to sustain cellular homeostasis (Borella *et al.,* 2014*;* Fukao *et al*., 2019). This metabolic flexibility supports temporary survival until oxygen availability improves.

The observed genetic variation underscores the potential for breeding mung bean genotypes with improved flooding tolerance (Table 6). Moderate-to-high heritability values for yield and root traits suggest genetic factors significantly influenced the responses to stress conditions. Basavaraj's (2024) findings revealed root traits, such as total length and volume, were under substantial genetic control, consistent with the present findings that tolerant lines retain superior root morphology. The co-expression of yield retention, root resilience, and shoot biomass in mung bean genotypes G-6, G-14, and G-15 disclosed pleiotropic effects with tightly linked tolerance loci. This study systematically evaluates mung bean genotypes under flooding stress, combining yield, root traits, and heritability estimates to identify promising donor genotypes for future breeding.

From a breeding perspective in this study, the tolerant mung bean genotypes were the immediate candidates as donor parents. Incorporating genotypes G-6, G-14, and G-15 in hybridization programs offers a pathway to develop improved cultivars in combination with tolerance to high yield. Screening for root traits can serve as a secondary selection index while pod number and seed weight remain primary yield targets. Combining physiological screening with genomic tools, such as GWAS (genome-wide association studies) (Kyu, 2024) and root-system association mapping (Basavaraj, 2024), will accelerate the outcome. The partially tolerant mung bean genotypes also allow pyramiding complementary mechanisms, root system vigor, and shoot biomass retention into single cultivars for enhanced resilience under flooding stress conditions. Importantly, this study systematically evaluates Indonesian mung bean landraces under controlled flooding stress. It contributes novel insights into their potential use as genetic resources for breeding waterlogging-tolerant cultivars.

CONCLUSIONS

Flooding stress conditions markedly reduced mung bean growth and yield traits (*V. radiata* L.), particularly for pod number and root-related traits, with precise genotype by flooding interactions observed. Among the 15 mung bean genotypes, Kasu (G-6), Lokal Majenang (G-14), and Kutilang (G-15) consistently sustained their pod production, root development, and seed set under waterlogging, highlighting their significant tolerance. Moderate heritability for root length and weight indicates their value as selection criteria, whereas environmental effects considerably affect the seed and stover traits. Pod number and root traits can be reliable indicators for identifying tolerant lines in breeding programs. The tolerant mung bean genotypes represent promising donor material for developing resilient mung bean cultivars for flood-prone environments.

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