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Assessing Resistance to Powdery Mildew in Mung Bean: The Role of Phenolic Compounds and Phenylalanine Ammonia-lyase (PAL) Activity

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ABSTRACT

Powdery mildew caused by *Erysiphe polygoni* is one of the main pathogens on mung bean that causes significant yield loss. This study determined the agronomic performance and physio-biochemical activities of twelve mung bean genotypes under powdery mildew infection. The experimental design was arranged in a completely randomized block design with three replicates. Initial disease symptoms appeared 14 days after planting (DAP) and then progressed to 31.7% in the moderate genotype (Sampeong) and 87.2% in the susceptible genotype (G2). The study suggested no significant correlation between chlorophyll contents and the severity of powdery mildew in mung bean genotypes; however, the disease negatively affected the yield in susceptible genotypes. Total phenolic and flavonoid contents in leaves showed a positive relationship with disease severity and mung bean resistance in the G6 genotype, in Vima 1. and Sampeong cultivars. Our findings showed that the phenolic compounds including phenylalanine ammonia-lyase (PAL) and tyrosine ammonia-lyase (TAL) activities in the leaves were important factors for mung bean resistance to powdery mildew and this interaction impacted the growth and productivity of mung bean plants.

Keywords: Mung bean, phenolic, phenylalanine ammonia-lyase (PAL), powdery mildew

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INTRODUCTION

Powdery mildew is an obligate biotrophic pathogen caused by *Erysiphe polygoni* D.C. fungus. The incidence of powdery mildew increases particularly during the cool-dry season in Indonesia (Indiati, 2012). The initial disease symptom develops from the upper side of the leaves with white floury patches, then changes to brown. This disease

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causes significant yield and quality losses in several important crops, including legumes such as peas and mung beans (Pandey et al., 2018). Yield losses due to this disease have been reported up to 40% at the reproductive stages, but the damage can be more intense when the infection occurs at the seedling phase (Mishra et al., 2024). Currently, there are 55 superior mung bean cultivars have been released in Indonesia; however, no resistant cultivars against powdery mildew are available, although some cultivars showed their tolerance in the field. Screening approximately 4,000 mung bean accessions at the Asian Vegetable Research and Development Center (AVRDC) in Taiwan revealed that less than 12% exhibited resistance to powdery mildew, with only a small number classified as highly resistant over multiple years (Reddy et al., 1994). In Indonesia, several mung bean lines have been developed for their resistance against powdery mildew in the field using a naturally infected plant approach (Hapsari et al., 2018). In addition, resistance evaluation conducted under a controlled environment is needed to confirm repeatable and consistent results of the plant pathogen interaction analysis (Sillero et al., 2010). Until now, resistant assessments to powdery mildew infection in legumes under controlled conditions and certain qualitative scales are still limited.

Genetics and variability of mung bean resistance to powdery mildew have been studied (Kasettranan et al., 2009; Pavithra et al., 2023). However, there is limited information about the physiological and biochemical mechanisms of mung bean resistance to *Erysiphe polygoni*. During the pathogen infection, physiological, biochemical, and metabolites in plants are changed (Kaur, Bhardwaj, et al., 2022). The changes noted in plant reactions are greatly influenced by the plant's genotype, the specific pathogen involved, and the interplay between these elements. A study by Mohapatra et al. (2016) demonstrated that the levels of enzymes that scavenge reactive oxygen species (ROS), such as superoxide dismutase (SOD) and catalase, as well as the amounts of total phenols (TP) and malondialdehyde (MDA), increased in both resistant and susceptible plant genotypes after being infected with powdery mildew. In addition, research conducted by Soundhiriyan et al. (2018) found that susceptible genotypes impacted by powdery mildew showed higher levels of total phenols, proteins, and non-reducing sugars. Phenolic compounds play an important role as defense agents in plants (Kumar et al., 2020). They act as phytoalexins and phytoanticipins as well as perform structural defenses against pathogens that effectively inhibit microbial entry, restrict pathogen growth, and reduce oxidative stress caused by infections (Kaur, Samota, et al., 2022; Kumar et al., 2020). The production of phenolic compounds in plants is influenced by the activity of phenylalanine ammonia-lyase (PAL) (Barros & Dixon, 2020). Moreover, PAL plays a key role in activating the precursors needed for synthesizing lignin and salicylic acid (SA), both of which are essential for developing acquired systemic resistance (SAR) and act as a substrate for oxidative enzymes such as peroxidase and polyphenol oxidase (Ampofo & Ngadi, 2021; Wang et al., 2022). In this study, we observed the resistance of mung bean breeding lines from two different parents with different resistance to powdery

mildew, Vima 1 and Sampeong. Further analysis of the biochemical compounds present in infected plants and the relationship between these parameters and resistance to powdery mildew in mung beans was conducted.

MATERIALS AND METHODS

Plant Materials, Artificial Inoculation, and Disease Scoring

Ten mung bean breeding lines from nine generations (F9) with high productivity (> 2 t/ha) derived from the crossing of Sampeong and Vima 1 cultivars were assessed for screening against powdery mildew. The breeding lines and their parents were grown in pots (16 × 50 × 30 cm) filled with a mixture of soil and organic fertilizer (5:1 v/v) inside a greenhouse (8°02'50.0"S 12°37'31.7"E, 345 m above the sea level). The media was fertilized with the recommended dosage (12.5:25:0 NPK kg/ha). Each genotype was planted in triplicates. Artificial inoculation was conducted by harvesting *E. polygoni* conidia in distilled water using a fine brush and filtering to remove impurities. The inoculum was adjusted to 10^6 conidia/mL and Tween 20 (0.1 ml/100 ml solution) was added to the suspension. The suspension was then sprayed on the upper and lower leaf surfaces 14 days after sowing.

Disease Assessment and Evaluation of Growth and Yield Parameters

Disease assessment of powdery mildew was monitored a week after inoculation using rating scales of 0 to 5 as described by Reddy et al. (1994). Disease assessment was carried out by calculating the percentage of leaves impacted on a single plant. The number of samples used to observe disease progression, growth, and yield consisted of three plants per replication, resulting in a total of 9 plants for each genotype. Percent Disease Index (PDI) was calculated according to the following formula:

$$\text{PDI} = \frac{\text{Sum of grades}}{\text{Total number of leaves analyzed} \times \text{maximum disease grade}} \times 100$$

PDI was used to determine the resistance level of mung beans to powdery mildew. Genotypes with PDI = 0% were considered as immune (I), PDI = 1-30% was considered as Resistance (R), PDI = 31-50% was considered as Moderately Resistant (MR)/tolerant (T), and PDI > 51% was considered as Susceptible (S).

The area under the disease progress curve (AUDPC) was calculated for each genotype based on the standard scale's measurement of disease severity using the following formula:

$$AUDPC = \sum_{i=1}^{n-1} \left(\frac{y_i + y_{i+1}}{2}\right)(t_{i+1} - t_i)$$

Where y = disease severity, t = time (day), n= number of observations

Growth and yield parameters were determined per plant. The average plant height was determined 56 days after planting. Plant biomass (fresh weight/plant), and the average numbers of pods and grains were assessed at harvesting based on the genotype maturity.

Determination of Plant Defense-related Enzymes

Biochemical parameters of mung bean genotypes, including chlorophylls, Phenylalanine ammonia-lyase (PAL), Tyrosine ammonia-lyase (TAL), and total phenolic content, were measured 14 days after artificial infection. The treatments were performed in triplicate. The mung bean leaves were ground into a fine powder using a mortar and liquid nitrogen and then stored at -20°C for future research.

Chlorophyll Content

The amount of chlorophyll was measured by Lichtenthaler and Buschmann (2001). The 90% methanol (1:10 w/v) was used to extract 0.5 g of mung bean leaves, which was used to further dilute the samples (1:5 v/v). At 470 nm, 652.4 nm, and 665.2 nm, three distinct wavelengths were used to measure the absorbance values. The following equations were used to determine the concentrations of carotenoid and chlorophyll:

$$Chlorophyll\ a\ [Ch\ a](\mu g\ ml^{-1}) = (16.82 \times Abs_{665.2}) - (9.16 \times Abs_{652.4})$$

$$Chlorophyll\ b\ [Ch\ b](\mu g\ ml^{-1}) = (34.92 \times Abs_{652.4}) - (16.54 \times Abs_{665.2})$$

Phenylalanine and Tyrosine Ammonia-Lyase Activities

PAL and TAL activities were determined according to Dogbo et al. (2012). Mung bean leaves (0.5 g) were extracted with 0.1 M borate buffer (pH 8.8) (1:10. v/v). Following centrifugation, 3.5 mL of distilled water, 30 mM L-phenylalanine, and 300 mM sodium borate were combined with the supernatant. L-tyrosine was used in place of L-phenylalanine for the TAL assay. After 60 minutes of incubation at 30 °C, the absorbance values were then measured at 290 nm and 330 nm, respectively. The amount of coumaric acid for TAL and cinnamic acid for PAL produced per gram of fresh tissue per hour was used to measure the enzyme activities.

Total Phenolic and Flavonoids Content

The ground samples (0.5 g) were extracted with 80% methanol (1:10 w/v). The mung bean extract was then diluted in distilled water (1:60 v/v) and mixed with 250 µL Folin Ciocalteu's reagent, 750 µL sodium carbonate, and distilled water. The mixture was then incubated for 90 minutes, and the total phenolic content was measured at 765 nm (Yusnawan et al., 2021). The phenolic content was expressed as milligrams of gallic acid equivalents per gram of sample (mg GAE/g sample).

Total flavonoid was measured according to a method by Lee et al. (2011). As many as 2500 µL of distilled water and 15 µL $NaNO_2$ 5% were used to react with the mung bean extract. After six minutes of incubation, 300 µL of 10% AlCl3 was added to the mixture. Following the addition of 1000 µL of 1 M NaOH and 550 µL, the total flavonoid content was determined at 513 nm.

Statistical Analysis

Statistical analysis of the data was subjected to ANOVA using the R Studio software (R v.4.2.2), and mean values were separated by the LSD at a probability level of 0.05%. The correlation matrix and the principal component analysis (PCA) were also made using R Studio software.

RESULTS AND DISCUSSION

Disease Symptoms and Severity

The first signs of infected mung beans were white, powder-like spores on the upper surface of the leaves, which grew and spread to cover the entire leaf surface (Figure 1b-d). Under a light microscope, the type of conidial formation (single or chain) as well as the presence of fibrosin bodies could be observed on fresh leaves (Figure 1d). Mycelia were formed on the young plants within two weeks after planting. In heavy infections, mycelia covered most of the leaf surface and stems up to 100%. This led to significant photosynthetic area reduction, thereby causing leaf drying and early leaf fall. The development of disease symptoms varied among genotypes. Several genotypes performed a very low percentage of infected leaf area (Figure 1a), while moderately resistant genotypes limited the pathogen growth on the lower leaves and performed hypersensitive reactions and necrotic symptoms (Figure 1b). Meanwhile, on the susceptible genotypes, leaves were covered by powdery mildew blotches (Figure 1c).

The resistance to powdery mildew on mung bean was expressed by a low score of disease severity and prolonged the augmentation of disease incidence. Different genotypes responded differently to powdery mildew infection. In greenhouse conditions, initial disease symptoms appeared in the early stages of the vegetative phase at 14 DAP and developed in the older plants until they reached maturity. During this period, disease progress was recorded at weekly intervals (Table 1). From the initial observation, several genotypes, such as G1, G2, G4, G7, and G9, showed high disease severity. Another genotype of the G6 showed low severity at the beginning (1.1%), but it rose to 77.8% at 56 DAP. Only G5 and G8 exhibited low infection rates that were comparatively stable. Meanwhile, G2 and G3 performed high disease severity at the first rating and the severity rose to 87.2% in the G2 and only 52.8% in the G3 at 49 DAP.

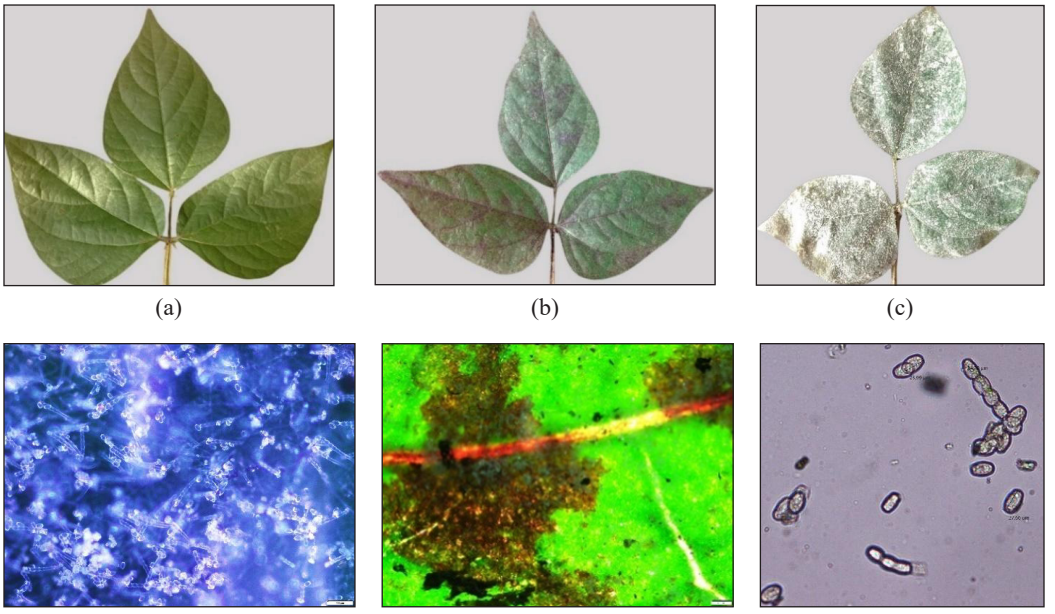


Figure 1. Mung bean leaves infected by powdery mildew: (a) No symptom; (b) moderate intensity; (c) and leaves covered by powdery mildew on susceptible genotypes; (d) micrographs of the powdery mildew fungi on the mung bean upper leaves; (e) hypersensitive reaction; (f) and chain of conidia

Table 1
Disease progress and resistant criteria of mung bean genotypes to powdery mildew

Genotypes	Disease Severity (%) 21 DAP	Disease Severity (%) 49 DAP	AUDPC	PDI	Resistant Criteria
G1	3.6 ± 1.3 ^{ab}	68.9 ± 7.6 $^{a-d}$	228.7 ± 33.4 $^{a-d}$	74.07	S
G2	4.6 ± 0.5 ^{a}	87.2 ± 5.2 ^{a}	289.3 ± 40.4 ^{a}	92.59	S
G3	4.8 ± 1.5 ^{a}	52.8 ± 9.8 $^{b-e}$	168.0 ± 26.3 $^{b-e}$	59.26	S
G4	2.6 ± 1.3 ^{ab}	73.3 ± 1.3 ^{abc}	247.7 ± 30.1 ^{abc}	77.78	S
G5	1.4 ± 0.8 ^{b}	43.3 ± 6.1 ^{cde}	146.6 ± 54.2 ^{cde}	48.15	MR
G6	1.1 ± 0.8 ^{b}	77.8 ± 2.1 ^{ab}	268.3 ± 41.8 ^{ab}	85.19	S
G7	4.4 ± 1.1 ^{a}	63.9 ± 6.7 $^{a-d}$	208.1 ± 51.9 $^{a-e}$	74.07	S
G8	1.2 ± 0.6 ^{b}	50.0 ± 8.3^{b-e}	170.7 ± 33.2 $^{b-e}$	59.26	S
G9	3.8 ± 1.1 ^{ab}	78.3 ± 2.3 ^{ab}	260.9 ± 38.2 ^{ab}	88.89	S
G10	2.8 ± 0.4 ^{ab}	42.2 ± 2.6 ^{de}	138.1 ± 43.7 ^{de}	48.15	MR
Vima 1	1.3 ± 0.8 ^{b}	51.7 ± 5.9 $^{b-e}$	176.2 ± 51.6 $^{b-e}$	55.56	S
Sampeong	1.6 ± 0.4 ^{b}	31.7 ± 6.4 ^{e}	105.4 ± 37.1 ^{e}	40.74	MR

Note. DAP = day after planting, AUDPC = area under the disease progress curve, PDI = percent disease index, S= Susceptible, MR = Moderately resistance. Values followed by the same letter within a column are not significantly different according to the Least Significant Difference (LSD) test ($p \leq 0.05$)

Based on the PDI analysis, none of the twelve mung bean genotypes exhibited resistance to powdery mildew. Three genotypes, namely Sampeong, G10, and G5 were classified as moderately resistant (MR). In contrast, the other nine genotypes were considered susceptible, showing PDI values higher than 50%. Moderately resistant genotypes showed chlorotic, limited sporulation, and exhibited a hypersensitive response. In the field tests, the Vima 1 cultivar was categorized as resistant to powdery mildew. However, when this cultivar was exposed to extremely high levels of stress in the greenhouse, the severity level rose to 51.7%, suggesting that this cultivar was susceptible. Meanwhile, the performance of the Sampeong cultivar against powdery mildew in this study was confirmed as moderately resistant, which was consistent with cultivar descriptions.

There were significant differences among the genotypes based on AUDPC values as shown in Table 1. The AUDPC values ranged from 105.39 to 334.40. Five genotypes (G1, G4, G6, G7, G9) had high AUDPC values as G2 genotypes, while low AUDPC values were observed in G3, G5, G7, G8, G10, Vima and Sampeong. At initial observation, five genotypes, including G5, G6, G8, Vima 1, and Sampeong, had disease severity lower than 2%. However, subsequent disease progression varied among genotypes. For instance, G6 disease severity was initially observed to be relatively low, but then disease progression increased rapidly, as indicated by a high AUDPC value. On the other hand, G3 was initially a relatively high severity, but subsequent observations revealed that the AUDPC value was comparatively low. This study showed that the crossing between Vima 1 and Sampeong, which was expected to inherit resistance traits, was not successful due to the new breeding lines being susceptible to powdery mildew.

Research by Rana et al. (2023) reported that resistance to powdery mildew in legumes was hereditary and could be passed down through hybridization. Variations in resistant responses to pathogens might arise from several factors, including environmental influences, durability of resistance, and pathogen virulence (Mundt, 2014). Notably, the powdery mildew observed in this study might be attributed to a new species or more aggressive populations of the pathogens. Kelly et al. (2021) reported that mung beans infected by two distinct pathogens, *Podosphaera xanthii* and *Erysiphe vignae*, exhibited similar symptoms but could only be differentiated through molecular methods. These two pathogens had not been reported to infect mung bean plants in Indonesia. Therefore, precise identification of the pathogens responsible for powdery mildew in Indonesia is essential. Unfortunately, molecular study related to the causal agents of the powdery mildew was not performed in this study. Furthermore, Sulima and Zhukov (2022) highlighted that even the strongest natural resistance to date is not universal, and previously effective alleles may lose their effectiveness against newly emerging pathogens, making taxonomic ambiguity and difficulties in identifying powdery mildew increasingly significant barriers for researchers and breeders.

Growth Performance and Yield

Powdery mildew affected the growth performance and yield of mung bean. There were significant differences among genotypes in terms of plant height and biomass as well as yield components (Table 2). Sampeong cultivar showed the highest plant height (68.0 ± 3.3 cm) and the lowest plant height was noted in G5 (37.1 ± 3.0 cm), G8 (38.0 ± 3.2 cm), G4 (40.0 ± 2.2 cm), Vima 1 (39.0 ± 1.5 cm), and G1 (41.0 ± 1.7 cm). However, plant height was dominantly affected by plant genetics rather than disease development. Disease severity was negatively correlated with plant biomass and yield. Powdery mildew, which infected from vegetative growth affecting generative growth, disrupting leaf development and causing premature defoliation. Consequently, the flowering process, formation, and pod filling were also affected. The highest yields were produced by G3 (15.6 ± 1.9 g), G5 (15.0 ± 6.5 g), G7 (14.9 ± 1.6 g), G8 (13.4 ± 0.9 g), G1 (13.4 ± 1.3 g), and Vima 1 (11.3 ± 0.2 g) genotypes, respectively. Meanwhile, the lowest yields were observed in Sampeong (7.6 ± 3.8 g), G4 (7.3 ± 1.8 g), G6 (8.8 ±6.7 g), G9 (9.4 ± 2.7 g), G10 (9.7 ± 0.6 g), and Vima 1 (11.3 ± 0.2 g) genotypes, respectively.

Powdery mildew infection also affected the yield quality as expressed by a reduced number of filling pods and seed weight as well as an increased number of empty or abnormal pods. The number of intact pods varied between 3.2 pods per plant (G10 genotype) and 7.6 ± 2.4 pods (G7 genotype). Although plant resistance did not directly influence the yield, low disease resistance affected the production of bean pods below their potential production (Basavaraja et al., 2020).

Table 2
Growth performance and yield components of mung bean genotypes infected by powdery mildew

Genotype	Plant height (cm)	Biomass (g)	Grain (g plant^{-1})	Number of Intact Pods per plant	Number of Empty Pods per plant
G1	41.0 ± 1.7 $^{d-g}$	69. 6 ± 5.5 ^{b}	13.4 ± 1.3 $^{a-d}$	6.7 ± 2.3 ^{ab}	3.9 ± 1.4 $^{a-d}$
G2	43.0 ± 3.5 $^{c-f}$	51.1 ± 5.0 ^{e}	14.1 ± 1.4 ^{abc}	5.3 ± 0.6 ^{abc}	5.4 ± 0.8 ^{ab}
G3	45.0 ± 4.2 ^{cd}	66.9 ± 1.1 ^{b}	15.6 ± 1.9 ^{a}	6.2 ± 2.0 ^{abc}	4.3 ± 2.0 ^{abc}
G4	40.0 ± 2.2 ^{efg}	55.8 ± 2.6 ^{de}	8.3 ± 1.9 ^{def}	4.0 ± 2.4 ^{bc}	5.7 ± 1.8 ^{a}
G5	37.1 ± 3.0 ^{g}	63.9 ± 2.4 ^{bc}	15.0 ± 6.5 ^{a}	5.1 ± 2.7 ^{abc}	3.9 ± 1.2 $^{a-d}$
G6	43.4 ± 4.9 $^{c-f}$	55.4 ± 6.7 ^{de}	8.8 ±6.7 $^{c-f}$	4.4 ± 2.9 ^{abc}	3.1 ± 2.7 ^{bcd}
G7	52.1 ± 2.3 ^{b}	90.2 ± 2.4 ^{a}	14.9 ± 1.6 ^{ab}	7.6 ± 2.4 ^{a}	1.8 ± 0.7 ^{d}
G8	38.0 ± 3.2 ^{g}	53.2 ± 5.7 ^{de}	13.4 ± 0.9 $^{a-d}$	5.3 ± 3.2 ^{abc}	3.3 ± 2.0 $^{a-d}$
G9	43.6 ± 2.6 ^{cde}	56.9 ± 2.7 ^{cde}	9.4 ± 2.7 $^{c-f}$	4.2 ± 1.9 ^{bc}	4.9 ± 1.4 ^{abc}
G10	47.4 ± 2.5 ^{bc}	53.3 ± 4.7 ^{de}	9.7 ± 0.6 $^{b-f}$	3.2 ± 0.8 ^{abc}	4.9 ± 0.5 ^{abc}
Vima 1	39.0 ± 1.5 ^{fg}	58.5 ± 2.5 ^{cd}	11.3 ± 0.2 $^{a-f}$	5.6 ± 2.1 ^{abc}	4.7 ± 1.2 ^{abc}
Sampeong	68.0 ± 3.3 ^{a}	86.5 ± 4.7 ^{a}	8.0 ± 4.1 ^{ef}	6.2 ± 2.2 ^{abc}	3.3 ± 1.9 $^{a-d}$

Note. Values followed by the same letter within a column are not significantly different based on the Least Significant Difference (LSD) test ($p < 0.05$)

Effect of Powdery Mildew Infections on Plant Pigments and Defence-related Enzymes

The chlorophyll content in mung bean plants infected with powdery mildew varied among different genotypes (Figure 2). The total pigments were from 0.73 µg g^{-1} (G10 genotype) to 1.33 mg g^{-1} (G7 genotype). Recent findings indicated that the correlation between chlorophyll content and the severity of powdery mildew in mung beans depended on genotypes. Some genotypes with lower disease severity, such as G4, G6, and G9 genotypes, exhibited higher chlorophyll levels compared to the G10 and Sampeong cultivars, which had relatively lower AUDPC values and disease severity. Conversely, G1, G2, and G7

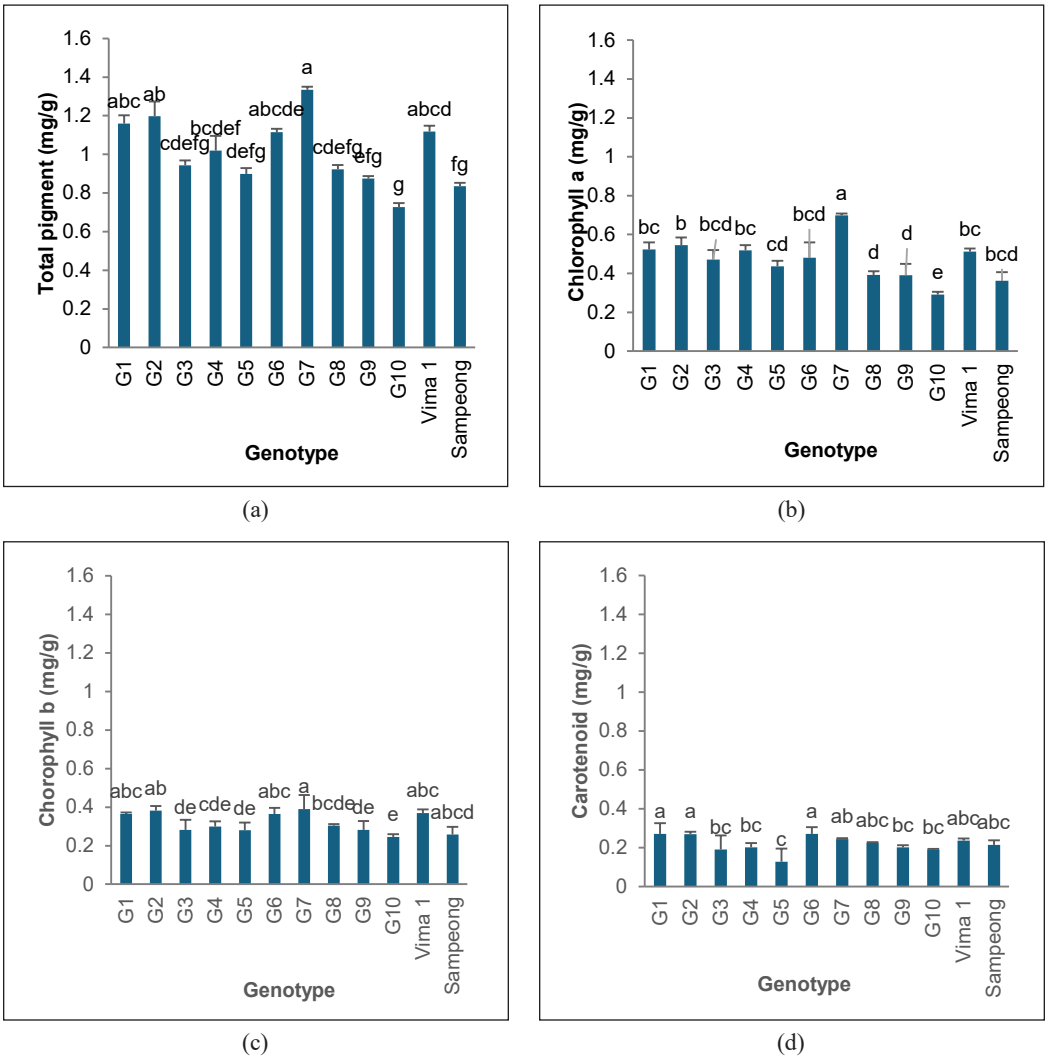
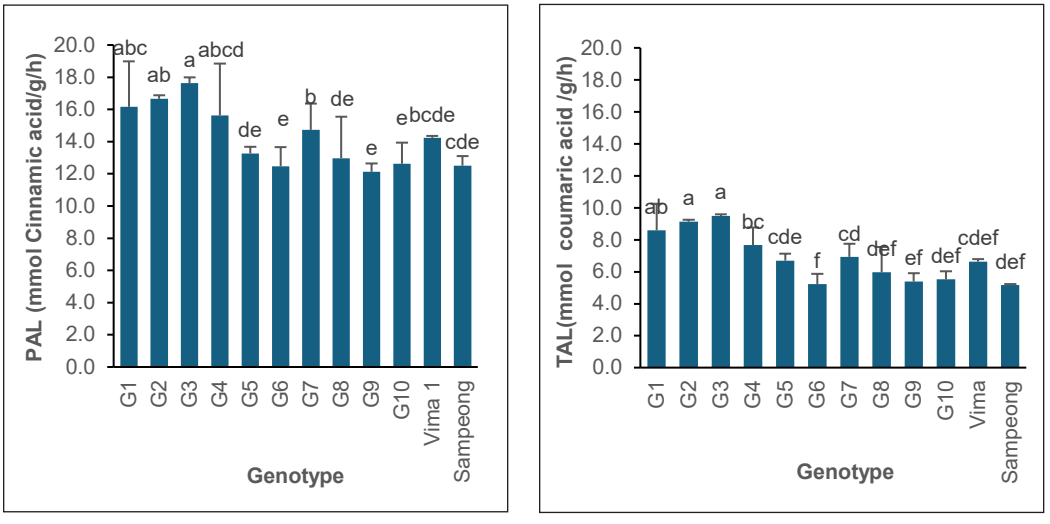


Figure 2. Mung bean genotypes infected by powdery mildew: (a) Total pigment; (b) chlorophyll a concentration; (c) chlorophyll b concentration; and (d) carotenoid

genotypes, which showed moderate disease severity and higher AUDPC values, also showed elevated chlorophyll content. Research conducted by Alwutayd et al. (2023) showed negative correlations between the severity of powdery mildew and the levels of chlorophylls a, b, and carotenoids in wheat. However, another study by Lobato et al. (2010) revealed that *Colletotrichum lindemuthianum* infection did not affect the contents of chlorophylls a and b in bean leaves. These findings suggested that both the type of pathogen and the plant species could influence chlorophyll levels in leaves.

Biochemical analyses showed that the enzyme activities associated with the defense mechanism varied among different genotypes. This study demonstrated a positive correlation between PAL and TAL activities in mung bean genotypes during powdery mildew infection. The concentration of PAL in the infected mung bean genotypes was higher than that of TAL. The G3 genotype exhibited relatively high activities for both enzymes, measuring 17.6 ± 0.4 mmol/g/FW/h for PAL and 9.5 ± 0.1 mmol/g/FW/h for TAL (Figure 3). Conversely, relatively low accumulation of PAL was observed in the G9 (12.1 ± 0.05 mmol/g/FW/h) and relatively low TAL activity was observed in the G6 (0.52 ± 0.06 mmol/g/FW/h). Phenylalanine ammonia-lyase and tyrosine ammonia-lyase are two critical enzymes involved in the pentose phosphate pathway (PPP). These two enzymes are essential for synthesizing defense-related secondary metabolites (Barros & Dixon, 2020). Both PAL and TAL can be induced in response to pathogen infections, and their coordinated activity can significantly enhance plant resistance to pathogens (Wang et al., 2022).

An assessment was conducted to determine whether variations in PAL and TAL activities correlated with the resistance of mung bean genotypes to powdery mildew. The



(a) (b)

Figure 3. Mung bean genotypes in response to powdery mildew infection: (a) Phenylalanine ammonia-lyase; (b) and Tyrosine ammonia-lyase

study found a dynamic relationship between PAL and TAL activities and the resistance of mung bean genotypes to powdery mildew. This was shown by disease severity and AUDPC values. Most genotypes with severe powdery mildew infections and high AUDPC values exhibited significantly high PAL and TAL activities. High levels of phenylalanine ammonia lyase (PAL) and tyrosine ammonia lyase (TAL) are typically associated with plant defense mechanisms; however, their relationship with increased disease occurrence indicates potential complex regulatory or mechanistic imbalances. These may arise from temporal discrepancies in the timing of defense activation (Boonchitsirikul et al., 1998), disrupting in metabolic channeling (Jun et al., 2018), and pathogen-derived counter-defense strategies (Kunkel & Brooks, 2002). In such cases, delayed activation of defense enzymes may allow pathogens to establish infections prior to the full mobilization of host defenses, potentially inhibiting downstream defense signaling pathways despite elevated PAL/TAL activity. Ten of the twelve genotypes showed a positive correlation between PAL and TAL activities with disease severity. The G3 genotype demonstrated low disease severity and slow disease progression but maintained high PAL and TAL activities. In contrast, G9 showed low PAL and TAL activities despite being severely infected by the pathogen. These results suggested that genotypes played a crucial role in the accumulation of PAL and TAL. Previous research by Mahatma et al. (2021) highlighted variations in PAL and TAL activities between resistant and susceptible groundnut genotypes during *Alternaria* leaf blight infection. Similar findings in PAL and TAL variants were observed in barley infected by stripe rust (Singla et al., 2020) and pepper infected by viruses (Sran et al., 2023).

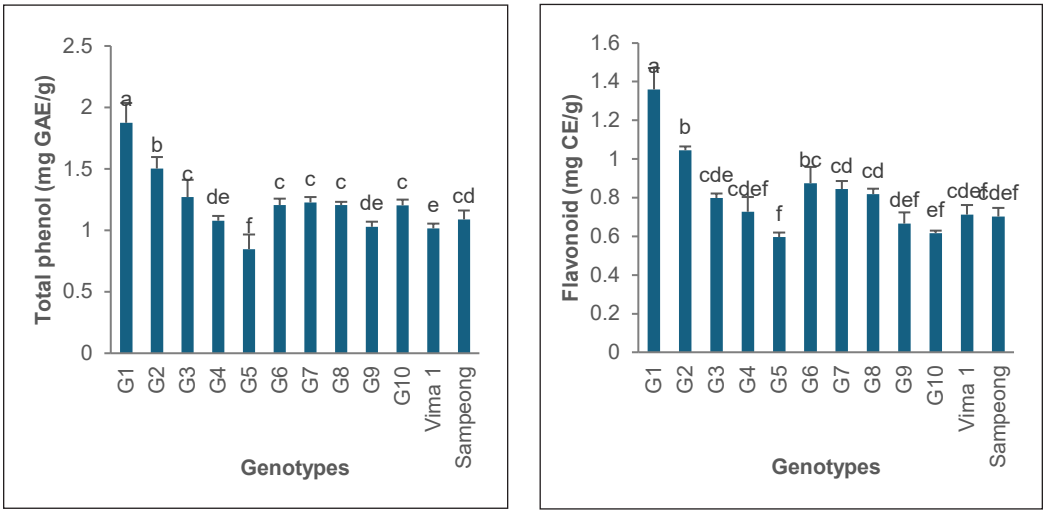
Powdery mildew infection led to an increase in the total phenolic content (TPC) of mung bean genotypes. There was a significant variation in TPC among mung bean genotypes infected by powdery mildew (Figure 4a). The total phenolic content in the mung bean genotypes ranged from 0.84 mg GAE g^{-1} to 1.88 mg GAE g^{-1}, with the highest levels observed in the G1 genotype and the lowest in the G5 genotype. Elevated total phenolic accumulation in mung bean genotypes that were severely infected by the necrotrophic pathogen *Erysiphe polygonii* represented a plant response to suppressing the pathogen development. The stimulation of phenolic compounds was directly triggered when plants recognize the potential pathogens, and it was interconnected with disease resistance against fungal plant pathogens (Kaur, Samota, et al., 2022).

Our study showed that high phenolic accumulation was not consistently related to suppressing the development of powdery mildew disease as indicated by high AUDPC values. On the other hand, low phenolic accumulation in genotypes with low disease incidence was also observed. This was possibly due to reprogramming of the phenylpropanoid pathway to accumulate certain phenolic compounds. Differences in phenolic accumulation in plants can be influenced by plant genotype. As reported by Ampofo and Ngadi (2021), common beans (*Phaseolus vulgaris*) had variations in phenolic

concentration depending on the cultivar and growing conditions. Different plant genotypes could affect the phenolic content in leaves due to variations in gene expression involved in the biosynthesis of phenolic compounds. This variation caused differences in the quantity and quality of phenolic compounds produced (Yeluguri et al., 2022). The current study revealed that the highly infected genotype (G1 and G2) had higher total phenolic contents. On the other hand, G4 and G9 genotypes exhibited high disease severity and AUDPC values, but low accumulation of total phenolic contents. The G5 genotype showed both low AUDPC value and low total phenolic content.

In addition to TPC, changes in one of the polyphenolic groups, namely flavonoids, were also observed. The results showed that powdery mildew infection affected the total flavonoid contents in mung bean leaves (Figure 4b). High concentration of total flavonoids was observed in susceptible genotypes, G1 and G2, measuring approximately 1.36 ± 0.11 mg CE g^{-1} and 1.06 ± 0.02 mg CE g^{-1}, respectively. Conversely, low quantity of flavonoid content was observed in moderately resistant genotypes, G5 (0.59 ± 0.02 mg CE g^{-1}) and G10 (0.62 ± 0.01 mg CE g^{-1}). A similar genotype trend was also observed in total phenolic contents. Although in the Sampoeng cultivar which was also resistant, there was a positive correlation between TPC and flavonoids with the disease severity.

Several studies have documented higher levels of phenolic and flavonoid groups in resistant genotypes compared to susceptible ones during infections caused by foliar diseases (Ramaroson et al., 2022; Reddy et al., 1994; Soundhiriyan et al., 2018). The lower flavonoid and total phenolic contents in resistant genotypes compared to susceptible ones could be explained by the activation of efficient alternative defense mechanisms



(a) (b)

Figure 4. Mung bean genotypes infected by powdery mildew: (a) Total phenolic contents; and (b) flavonoid contents

and rapid response strategies. The mechanism prioritized direct resistance rather than the accumulation of these compounds (Yeluguri et al., 2022). Flavonoids play a key role in defense mechanisms mainly through increased levels of protective compounds such as isoflavones and phytoalexins (Ramaroson et al., 2022).

Correlations Between Defense-Related Enzymes and Mung Bean Growth and Yield

A principal component analysis (PCA) and a correlation study on defense parameters and plant growth were carried out to determine the direct or indirect influence of the measured defense enzymes on plant growth and yield. Pearson's correlations showed that all defense parameters and plant pigments, namely PAL, TAL, phenolics, flavonoids, and chlorophyll content, had a positive correlation with the growth and yield of mung bean genotypes (Figure 5). The correlation analysis showed that flavonoids positively correlated with total phenolic content (r=0.89), PAL (r=0.56), and TAL (r=0.59). Furthermore, there were differences in the relationship between flavonoids and the severity of the disease, which were impacted by various factors such as plant species and genotypes. The current study showed that flavonoid accumulation in the G1 genotype was high, in line with disease severity and disease progress. In addition, several genotypes of G2, G3, G5, G7, G8, Vima 1, and Sampeong showed high flavonoid accumulation and low AUDPC values. Wang et al. (2022) stated that several flavonoids are classified as phytoalexins due to their accumulation in plant tissues upon pathogen infection; therefore, the increase in concentration triggers increasing plant resistance. Another similar study conducted by Steinkellner and Mammerler (2007) showed that a low increase in flavonoid concentrations exhibited antimicrobial properties against *Fusarium oxysporum* f. sp. *lycopersici*. Thus, it is also interesting to observe a comprehensive mechanism of genotypes with higher flavonoid and phenolic contents as well as higher PAL and TAL activities against powdery mildew infection.

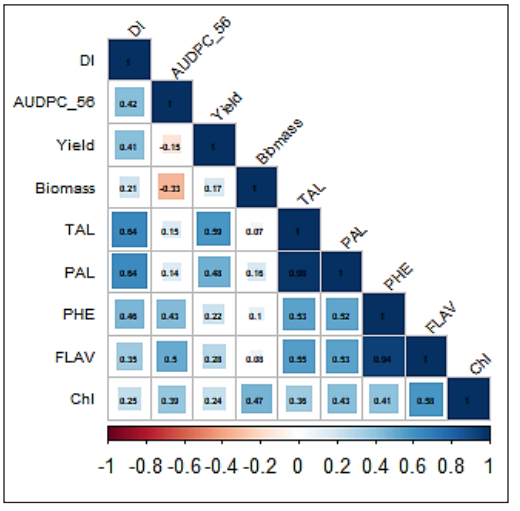


Figure 5. Matrix correlation of growth parameters yields and its related traits. IP: intact pods, FEN: total phenolic content, FLAV: total flavonoid content, PAL: PAL activity, TAL; TAL activity, AUDPC: AUDPC at 56 DAP

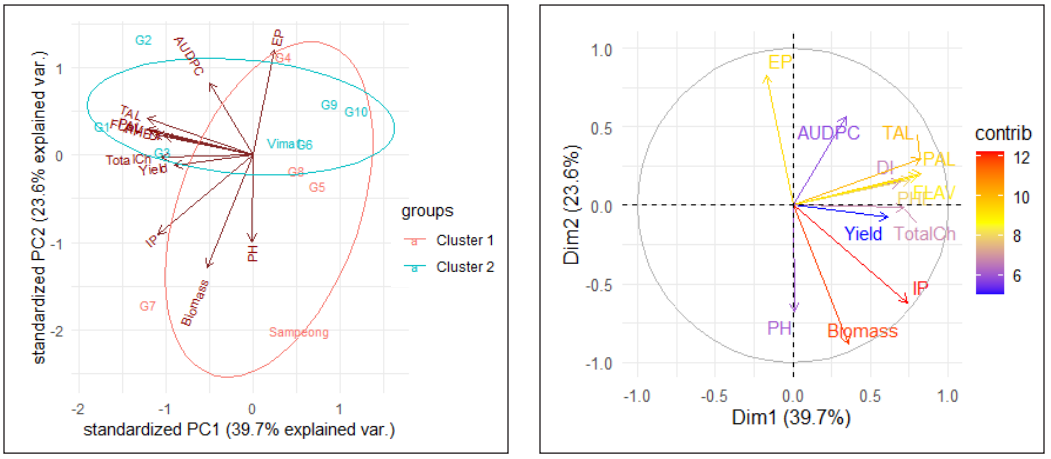
PAL was positively correlated with yield (r=0.62) and number of filled pods (r=0.52). However, there was no correlation with plant biomass. Apart from being reported to play an important role in plant resistance mechanisms, PAL also influenced

plant growth, such as the formation and development of roots and the addition of biomass (Cass et al., 2015). Total phenolic and flavonoid contents also play a crucial role in plant growth and development. A study conducted by Shen et al. (2022) revealed that flavonoids played essential roles in numerous biological processes, such as plant development, growth, and ripening. Another study by Tanase et al. (2019) highlighted the impact of several physiological processes involved in plant growth and development, including the synthesis of photosynthetic pigments, cell division, flower development, and seed germination. Interestingly, a positive correlation between chlorophyll content and the number of seeds (yield) as well as filled pods was observed. Chlorophylls play a crucial role in photosynthesis, which affects plant development and productivity. Surprisingly, severe powdery mildew infection on several mung bean genotypes had high chlorophyll content; however, it negatively affected the seed yield. This was in line with several previous studies, which stated that high chlorophyll contents did not correlate with high yields due to various physiological and environmental factors. These factors affected plant performance such as the allocation of energy and nutrient resources to produce defense compounds (Li et al., 2023).

Principal Component Analysis (PCA) was conducted on data related to mung bean growth and yield, disease severity, and the activity of defense-related enzymes (Figure 6a). The first principal component (PC1) accounted for 39.7% of the overall variation, with two variables linked to disease susceptibility, namely AUDPC and DI, showing significant contributions. The second principal component (PC2) explained 23.6% of the variation, with variables related to resistance mechanisms, such as TAL and PAL, exhibiting strong impacts on PC2.

The relationships among these four resistance-related variables indicated a positive correlation, suggesting that the activities of defense-related enzymes tent to increase simultaneously. In the PCA biplot, all mung bean genotypes were spread across all quadrants, revealing certain clustering patterns. In terms of resistance to powdery mildew, genotypes with elevated PC1 scores, such as G1 and G2, exhibited high DI and AUDPC values, suggesting a higher susceptibility to the disease. In contrast, genotypes such as Sampeong and G10, positioned far from the vectors related to disease and negatively correlated with PC1, were likely more resistant to powdery mildew.

The contributions of each variable to the PCA were shown in Figure 6b. Variables particularly TAL, FLAV, and plant height (PH) accounted for the most significant contributions (marked in red/orange) to Dimension 1 (Dim 1). PAL and FLAV notably influenced the positive direction of Dim 1, while biomass and plant height had a strong influence on its negative direction. These variables could serve as essential indicators for differentiating genotypes based on the growth characteristics and phytochemical contents. Variables such as the number of empty pods (EP; yellow color) showed moderate



(a) (b)

Figure 6. (a) Principle component analysis (PCA); and (b) contributions of 12 trait measurement variables to the first 2 dimensions of the principal components analysis of mung bean leaves. The first dimension (Dim1) is composed primarily of biochemical traits related to mung bean resistant (PAL, TAL, PHE, FLAV), and the second dimension (Dim2) is composed primarily of resistant variables traits (AUDPC, DI). EP: empty pod; DI: disease incidence; Tot Ch: total chlorophyll, PH: plant height, IP: intact pods, FEN: total phenolic content, FLAV: total flavonoid content, PAL: PAL activity, TAL: TAL activity, AUDPC: AUDPC at 56 DAP

contributions, whereas yield (indicated in blue) had weaker contributions due to its negative correlation with Dimension 2 (Dim 2). The PCA revealed a distinct relationship between genotype traits and disease resistance. The clustering of genotypes based on PCA could be used in selecting superior varieties by considering both disease resistance and agronomic attributes such as yields.

Our research indicated that the resistance of mung beans to powdery mildew was affected by the physiological and biochemical states of the plants during the pathogen infection process. *Erysiphe polygoni*, a biotrophic pathogen, requires tissue penetration for survival and growth. Consequently, effective resistance strategies involve inhibiting the pathogen entry into the tissue through structural barriers such as lignin and the activation of systemic acquired resistance (SAR). Thus, the rapid accumulation of total phenolics at elevated levels is crucial for the resistance mechanism against powdery mildew. Genotypes that respond quickly to increased phenolic compounds exhibit greater resistance compared to those that respond slowly. Furthermore, a swift rise in PAL activity is essential since this enzyme is vital for initiating the synthesize of lignin and salicylic acid (SA). Both of which are critical for establishing acquired systemic resistance (SAR) and serve as substrates for oxidative enzymes such as peroxidase and polyphenol oxidase. Therefore, a breeding strategy can be implemented that focuses on selecting genotypes with inherent and swift induction of PAL/TAL expression following infection to guarantee prompt defense activation.

CONCLUSION

None of the genotypes from the Vima 1 and Sampeong cultivar progeny exhibited high resistance to powdery mildew disease. However, two selected genotypes of G10 and G5 were identified moderately resistance, suggesting some levels of defense capability against this pathogen. The PAL and TAL enzymes, along with the accumulation of total phenolics, were crucial components of the defense response in mung bean to powdery mildew infection. It was noteworthy that the effectiveness of these biochemical responses varied among different genotypes, highlighting the complexity of resistance mechanisms in mung beans. Based on our findings, it was suggested that the resistance mechanism in mung bean against powdery mildew primarily followed the phenylpropanoid pathway with the roles of PAL, TAL, and phenolic content. In addition, marker-assisted selection, particularly phenylpropanoid pathway genes may be taken into account for mung bean breeding resistance against powdery mildew.

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