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ORIGINAL RESEARCH PAPER

Exploring agronomic diversity and disease tolerance in soybeans to combat Cowpea mild mottle virus

H. Kuswantoro[1], S. Zubaidah[2,*], E. Uge[1], K. Rozana[2], Purwantoro[1], J. Purnomo[1]

[1] Research Center for Food Crops, Research Organization for Agriculture and Food, National Research and Innovation Agency, Jl. Raya Jakarta-Bogor, Bogor 16911, West Java, Indonesia

[2] Department of Biology, Faculty of Mathematics and Natural Sciences, State University of Malang, Jl. Semarang 5 Malang 65145, East Java, Indonesia

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ABSTRACT

BACKGROUND AND OBJECTIVES: The yield of soybeans is affected by the performance of agronomic traits and the presence of abiotic and biotic environmental stresses. The utilization of pesticides to alleviate biotic environmental stressors results in environmental deterioration. One of the biotic environmental stresses is virus disease caused by Cowpea mild mottle virus. Identifying the main factors influencing yield and selecting traits resistant to virus infection can assist development programs in creating soybean varieties with enhanced Cowpea mild mottle virus tolerance. The soybean lines can face one of the biotic environmental stresses. Soybean varieties are susceptible to a range of biotic environmental challenges. This investigation sought to examine the diversity in agronomic traits and disease resistance, to identify the top-performing soybean varieties for controlling Cowpea mild mottle virus disease.

METHODS: The plant materials were 1000 soybean lines originating from 26 crosses. Each line was planted in rows and inoculated with Cowpea mild mottle virus naturally using the Bemisia tabaci vector. To set up the experiment, a population of Bemisia tabaci carrying the Cowpea mild mottle virus was established in the field, enabling natural biotic environmental stress of the plants by the virus infection. The identification of the lines was conducted through an assessment of agronomic characteristics and an analysis of the relationship between these characteristics and their susceptibility to Cowpea mild mottle virus. The attributes that had a substantial impact on the principal component analysis biplot and their correlation with seed yield per plot were initially identified as selection criteria.

FINDINGS: Soybean plants displayed diverse agronomic characteristics and disease ratings. Rather than relying on resistance, their defense mechanism against diseases involved tolerance. The variation in soybean characteristics can be attributed mainly to factors such as seed yield, the number of filled pods, and the number of productive pods per plant. Additionally, plant height showed the strongest correlation among these traits. The selected 100 soybean varieties displayed outstanding agronomic characteristics and resistance to diseases, leading to a decrease in the need for pesticides and contributing to environmental conservation.

CONCLUSION: Soybean seed yield is influenced by agronomic traits and biotic environmental stress such as virus disease, with significant diversity observed among the tested lines. The attributes that had the most significant impact were the number of productive nodes, quantity of filled pods, and seed yield per plant. Plant height consistently showed a strong correlation with seed yield. Seed yield per plant had a positive correlation with the disease score, making it unsuitable as a selection criterion. This positive correlation has been observed, indicating that soybeans possess a mechanism of tolerance that enables them to sustain optimal seed yields even when infected by a virus. The criteria for selecting 100 superior soybean lines included the number of filled pods, number of nodes, and plant height, which were deemed suitable for the evaluation process. The use of 100 selected soybean lines can reduce pesticide usage while maintaining environmental quality and supporting sustainable agriculture.

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62	9	2

*Corresponding Author:
Email: *siti.zubaidah.fmipa@um.ac.id*
Phone: +62 813 3443 5234
ORCID: 0000-0002-0718-6392

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INTRODUCTION

Excessive utilization of chemicals poses a significant threat to the environment as it has the potential to lead to the development of resistance to diseases (Varah *et al.,* 2024). Over time, the efficacy of pesticides may be diminished by pathogens that acquire resistance mechanisms (Hawkins *et al.,* 2019). Resistant diseases can only be overcome by the use of stronger and more abundant chemicals. Excessive use of pesticides can also kill non-target organisms, including insects and beneficial microorganisms (Serrão *et al.,* 2022). Prolonged utilization of pesticides significantly influences the expenses associated with environmental management (Varah *et al.,* 2024). The use of disease-resistant soybean varieties is one strategy for sustainable management of plant diseases (Nelson *et al.,* 2018). Soybean cultivars with resistance to diseases have the potential to lower both the frequency and intensity of disease outbreaks (Lin *et al.,* 2022). The need for pesticides will decrease as the incidence of disease decreases. Reducing the use of chemicals has a positive impact on the environment, including reducing soil contamination (Siregar *et al,* 2024), water contamination (Kuppusamy *et al.,* 2024), surface water eutrophication (Liu *et al.,* 2021), maintaining soil nutrient cycles by soil microorganisms (Pedrinho *et al.,* 2024), and lowering human health risk (Korrani *et al.,* 2023). The reduction in pesticide usage has the potential to support biodiversity conservation by promoting the successful reproduction of beneficial organisms (Bartling *et al.,* 2024). Plant disease management can be conducted more holistically and sustainably through the integration of disease-resistant soybean varieties. Many viruses are known to infect soybeans, one of which was the Cowpea mild mottle virus (CpMMV). CpMMV infection in soybeans can cause plant height, pod number, and seed size, and yield losses between 174-638 kilogram per hectare (kg/ha) (da Silva *et al.,* 2020). The severity and type of disease can fluctuate based on a variety of factors including climate conditions, length of growing season, management of disease-causing agents, genetic variability, and plant variety (Lin *et al.,* 2022). There are no CpMMV-resistant varieties available in Indonesia. High-yielding varieties can be achieved through the identification of resistance in soybean lines and the assessment of their agronomic performance. Several genotypes have superior agronomic, anatomical, and morphological characteristics against CpMMV attacks (Zubaidah *et al.,* 2023a). The aforementioned lines have the potential to serve as a valuable genetic reservoir for the development of soybean plants that are resistant to CpMMV through breeding efforts. Strategies for plant's defense against infectious diseases are divided into resistance and tolerance. Plant resistance depends on the ability of the host to kill the pathogen, whereas tolerance improves host health while having a neutral to positive influence on pathogen robustness (McCarville and Ayres, 2018). Tolerance can also be described as the ability of a particular variety to produce a higher yield than another variety when facing comparable disease severity (van den Berg *et al.,* 2017). Tolerance is predicted to cause changes in the pathogen's virulence and rates of multiplication (Pagán and García-Arenal, 2020). Tolerance to disease is dependent not only on host cells and metabolism but also on host health (McCarville and Ayres, 2018). In addition to other mechanisms, disease tolerance can be achieved through the establishment of mechanical barriers within the cuticle and host cell walls, leading to a reduction in disease severity in plant species (Song *et al.,* 2021). The plant genotype and environment affect both tolerant and resistant mechanisms, producing unique results that may be sensitivity, tolerance, or resistance (Baebler *et al.,* 2020). Developing soybean varieties with resistance to pathogens is an effective strategy within sustainable soybean breeding programs, ultimately leading to enhanced crop yields (Lin *et al.,* 2022). Identifying key factors that contribute to yield and selecting traits that are resistant to CpMMV virus infection can help develop programs for soybean varieties with superior CpMMV-resistant traits. Further studies might focus on analogous themes, yet employ genetic material that differs from that of the current study. Disparities in genetic material can lead to divergent research findings as a result of the varying responses exhibited by each genetic material towards environmental factors, including reactions to CpMMV attacks. Besides, the agronomic data of previous studies was few. Much research may have focused on the virus itself or chemical control techniques. A total of 1000 soybean lines were chosen in prior studies through individual selection, focusing on agronomic traits and disease ratings (Zubaidah *et al.,* 2023b). The use of selected soybean lines is expected to reduce pesticide

use. This study was designed to explore agronomic diversity and plant's tolerance to CpMMV disease. The current study aims to explore the agronomic characteristics and disease tolerance of 1000 F6 generation soybean lines and to select 100 soybean lines based on the contribution of agronomic traits and the correlation between those traits.This study has been carried out in Malang Regency, East Java, Indonesia in 2023.

MATERIALS AND METHODS

Plant materials

The utilization of plant materials plays a crucial role in achieving favorable outcomes in research endeavors, particularly in the process of selecting suitable lines. One thousand F6 soybean lines were used for plant materials. These lines were generated from 26 crosses. The parents of the cross were large-seed soybean varieties and CpMMV-resistant soybean lines. The large-seed soybean varieties were Panderman, Grobogan, Burangrang, and Argomulyo. The CpMMV-resistant soybean lines were UM 7.6, UM 7.2, UM 6.3, UM 6.2, UM 6.1, UM 4.1, UM 3.4, UM 3.2, and UM 2.4. The 26 soybean crosses were Argomulyo x UM 6.3 (crossing Argomulyo with UM 6.3, the code is A), Burangrang x UM 3.4 (crossing Burangrang with UM 3.4, the code is B), Burangrang x UM 4.1 (crossing Burangrang with UM 4.1, the code is C), Burangrang x UM 7.2 (crossing Burangrang with UM 7.2, the code is D), Burangrang x UM 7.6 (crossing Burangrang with UM 7.6, the code is E), Grobogan x UM 2.4 (crossing Grobogan with UM 2.4, the code is F), Grobogan x UM 3.2 (crossing Grobogan with UM 3.2, the code is G), Grobogan x UM 3.4 (crossing Grobogan with UM 3.4, the code is H), Grobogan x UM 4.1 (crossing Grobogan with UM 4.1, the code is I), Grobogan x UM 6.1 (crossing Grobogan with UM 6.1, the code is J), Panderman x UM 3.4 (crossing Panderman with UM 3.4, the code is K), Panderman x UM 4.1 (crossing Panderman with UM 4.1, the code is L), Panderman x UM 6.2 (crossing Panderman with UM 6.2, the code is M), Panderman x UM 6.3 (crossing Panderman with UM 6.3, the code is N), UM 2.4 x Grobogan (crossing UM 2.4 with Grobogan, the code is O), UM 3.2 x Grobogan (crossing UM 3.2 with Grobogan, the code is P), UM 3.4 x Panderman (crossing UM 3.4 with Panderman, the code is Q), UM 3.4 x Burangrang (crossing UM 3.4 with Burangrang, the code is R), UM 4.1 x Argomulyo (crossing UM 4.1 with Argomulyo, the code is S), UM 4.1 x Burangrang (crossing UM 4.1 with Burangrang, the code is T), UM 6.1 x Argomulyo (crossing UM 6.1 with Argomulyo, the code is U), UM 6.2 x Argomulyo (crossing UM 6.2 with Argomulyo, the code is V), UM 6.2 x Panderman (crossing UM 6.2 with Panderman, the code is W), UM 6.3 x Burangrang (crossing UM 6.3 with Burangrang, the code is X), UM 6.3 x Panderman (crossing UM 6.3 with Panderman, the code is Y), UM 7.6 x Burangrang (crossing UM 7.6 with Burangrang, the code is Z).

Study site

The study site determines plants' growth because plants have prerequisites for optimal growth. The study took place at coordinates 8.05568 latitude, 112.66675 longitude, and an altitude of 478 meters (m) in the Village of Srigading, District of Tajinan, Malang Regency, located in East Java, Indonesia. An augmented design was implemented in the experiment, with the planting taking place on June 13, 2023. The soybean lines were grown with a planting distance of 40 centimeters (cm) between rows and 20 cm between plants, with two plants per hill, and each line spanning 3 meters in length.

Soil tillage and fertilization

To achieve maximum growth, soybean plants require well-structured soil and adequate nutrients. The soil was carefully plowed in preparation for planting soybeans, ensuring an optimal environment for the plants to thrive. Drainage ditches were dug, and herbicides were applied to remove weeds before seeding. An application of 75 kilograms (kg) of calcium chloride (KCl), 75 kg of superphosphate (SP-36), and 50 kilograms of urea per hectare (kg urea/ha) is recommended for optimal fertilization.

Agronomic observation

The plants underwent evaluation for different parameters related to growth and productivity, including seed yield, seeds produced per plant, the weight of 100 seeds, the number of filled pods, the number of unfilled pods, the number of branches, plant height, days to maturity, and days to flowering.

Disease inoculation and observation

Disease inoculation is done to ensure the infection of the disease. To prepare for the experiment, a population of *Bemisia tabaci* carrying the CpMMV

was propagated during one growing season by planting soybeans around the area that will be used for research. Pesticides lethal to Bemisia tabaci were not utilized on the soybean strains intended for their propagation. This condition allowed *Bemisia tabaci* to be available in sufficient quantities to inoculate soybeans. As a result of the biotic environmental stress introduced during the experiment, the plants were able to undergo natural infection by the virus. The evaluation of the illness was conducted according to the standards set forth by Zubaidah and Kuswantoro (2016). Disease scoring took place 30 days post-planting and again at 50 days post-planting. The scoring system classified the diseases; healthy leaves with no mottling or yellow spots (score 1), yellow spots with non-wrinkled leaves (score 2), leaf spots with slight wrinkling and mild mosaic (score 3), yellow spots with wrinkling and clear mosaic but no necrosis (score 4), and yellow spots with wrinkling, clear mosaic, vein necrosis, malformations, and leaves becoming smaller and curving downwards and upwards (score 5).

Data analysis

Data analysis is conducted to condense a large amount of data and identify the necessary steps for interpretation. The histogram was done using Minitab14, the boxplot was illustrated with R program version 4.3.1., and the correlation was computed by using Microsoft Excel (MS Excel).

Selection criteria

Selection criteria are conducted to acquire soybean lines that exhibit specific desired characteristics. Before selection was carried out, the traits that had the greatest contribution to the principal component analysis (PCA) biplot and their correlation with seed yield per plot were first determined as selection criteria. The various characteristics were normalized through the use of z-scores to facilitate the selection process. One hundred top-performing soybean lines were chosen according to these specific criteria.

RESULTS AND DISCUSSION

Plant growth and productivity are limited by biotic environmental stress factors (Saddique *et al.,* 2018). The F6 lines exhibited a flowering age of 30-45 days after planting (DAP), with 15 lines achieving the shortest flowering age (Fig. 1a). The 15 lines belonged to a Q cross (UM 3.4 x Panderman) and one line belonged to a G cross (Grobogan x UM 3.2) with 30 DAP, while the longest days to flowering were achieved by G40, followed by G165 and G631, both with a flowering age of 40 DAP. The days to maturity (DTM) also varied ranging from 81-94 DAP (Fig. 1b). The longest DTM was achieved by G565, G568, G569, and G567 with 95 DAP, all of which came from an N cross (Panderman x UM 6.3) except G565 which came from an S cross (UM 4.1 x Argomulyo). The shortest DTM was achieved by G943, G944, G945, G946, and G947 which all came from the cross I (Grobogan x UM 4.1). The diversity observed in various crosses can be explained by the genetic differences between the parent plants used in the crosses. Numerous genetic factors have been discovered to regulate the timing of flowering, known as days to flowering (DTF) and days to maturity (DTM) (Khan *et al.,* 2022; Zhang *et al.,* 2015). These genes contribute to the variability in DTF

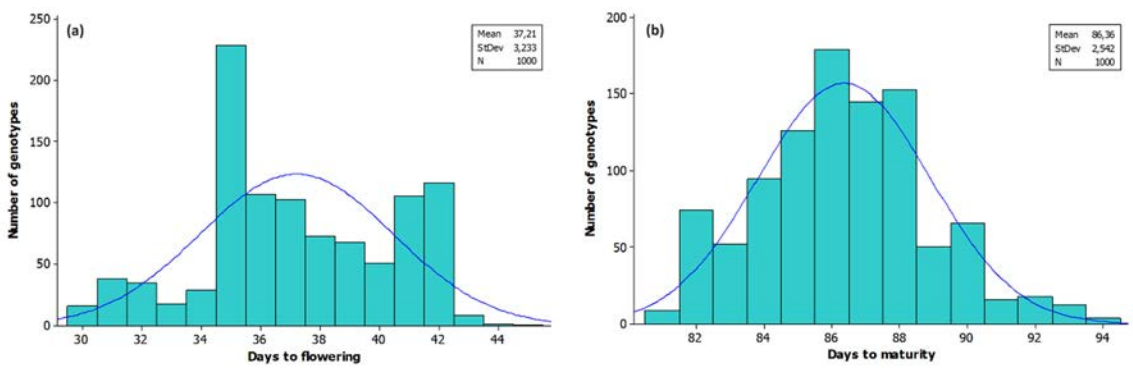


Fig. 1: Phenological traits of 1000 soybean lines originated from various crosses; days to flowering (a), days to maturity (b)

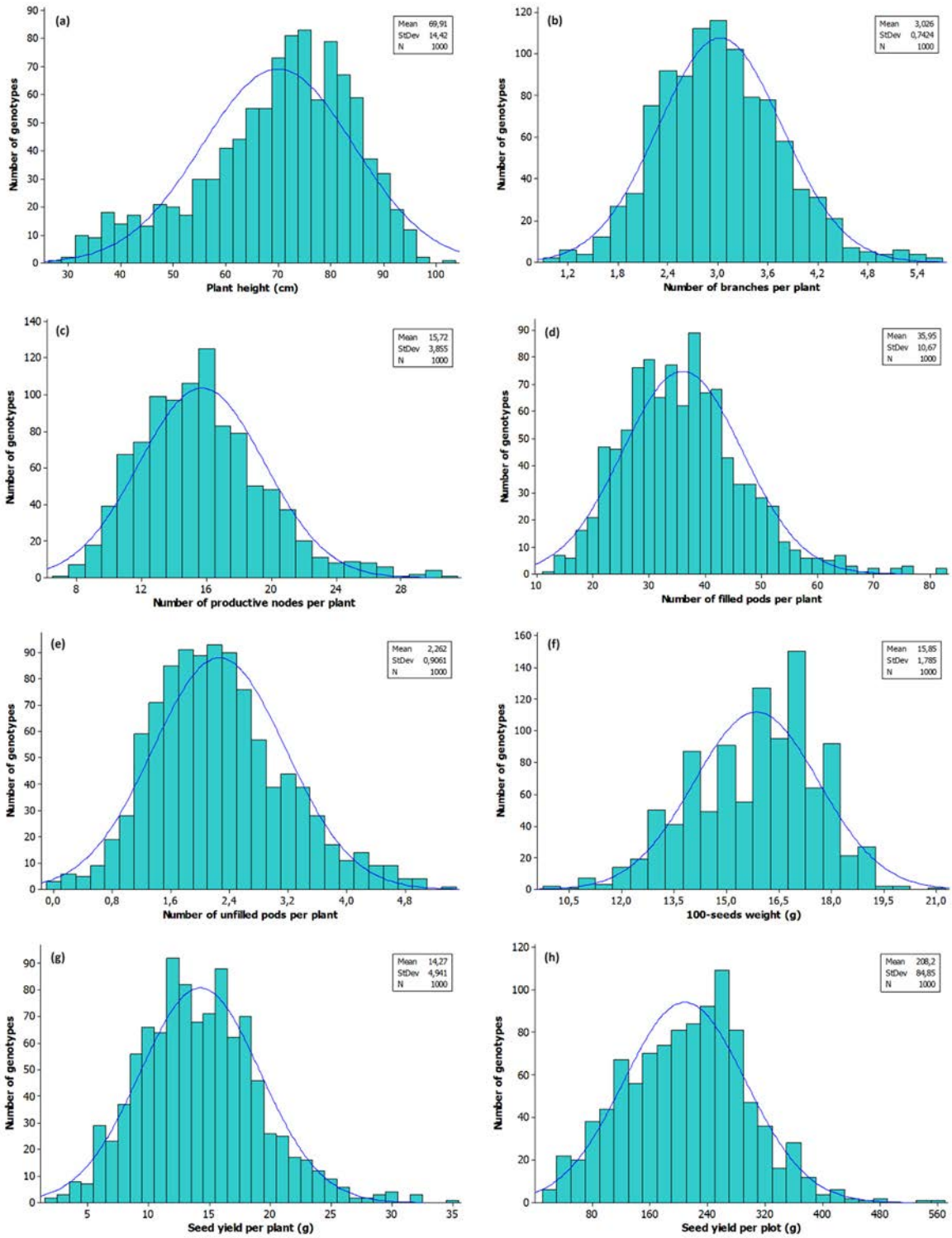


Fig. 2: Agronomic traits of 1000 soybean lines originated from various crosses

and DTM. Moreover, in the identical cross, diversity emerges from variances in the genetic constitution of the genotypes under examination. The DTF and DTM ranges in this study are different from the previous study (Zubaidah *et al.,* 2023b). The reason behind the differences in flowering schedules among various plant types is believed to stem from the distinct growing seasons they experience, with DTF and DTM being intricately linked to photoperiodicity (Xia *et al.,* 2021; Zhai *et al.,* 2022). Flowering age, apart from being an ecological indicator of photoperiodic response, is also an agronomic trait that influences seed yield, seed quality, and adaptability of soybeans (Hou *et al.,* 2023).

Plant height (HGT) exhibited a range of 27.60 to 103.4 cm, having a mean value of 69.9 cm (Fig. 2a). Among the plants, G26 from the cross I (Grobogan x UM 4.1) reached the highest height. The line with the lowest plant height was G919 from a U cross (UM 6.1 x Argomulyo) followed by G739 from a Q cross (UM 3.4 x Panderman). The height of a plant is a contributing factor to the overall yield of the plant. Plants that achieve ideal growth will consequently produce the best possible outcomes. Plant height with an average of 69.9 cm in this study is classified as optimal, which according to Yang *et al*. (2021) the ideal soybean plant height is 70-90 cm. Discrepancies among individual soybeans examined within the same cross or across different crosses are also evident in the HGT (Fig. 2). Crosses that provide a wide range of HGT were crosses I, O, Q, S, and T. In all of these crosses UM 4.1 was used as a parent except in cross O. It seems that UM 4.1 is a parent that contributes a wider range of HGT. Plant height is controlled by genes related to plant growth type (Miranda *et al.,* 2020), as well as multiple genes that are sensitive to environmental changes (Fang *et al.,* 2020) including meteorological factors and soil properties (Yang *et al.,* 2021). The branches exhibited a distribution pattern resembling that of a normal graph (Fig. 2b). The highest branch number was reached by G324 and G393, where these lines came from an S cross (UM 4.1 x Argomulyo), while the lowest branches were achieved by G923 from a P cross (UM 3.2 x Grobogan) and G919 from a U cross (UM 6.1 x Argomulyo). The UM 4.1 parent exhibited the highest number of branches per plant, specifically with the G324 and G393 lines from the S cross. In this cross UM 4.1 was the female parent, but the branch number was not controlled by maternal effects (Badiaraja *et al.,* 2021a). The environment, particularly plant density, plays a significant role in influencing the quantity of branches (Nakano *et al.,* 2019; Xu *et al.,* 2021). Generative traits generally formed a normal curve, but the slope of each graph was different. In general, the F6 lines reached the number of productive nodes (NOD) around 15 with the range of 6.8-30.6 nodes (Fig. 2c). Two lines had more than 30 nodes, namely G165 from an S cross (UM 4.1 x Argomulyo) and G77 from a P cross (UM 3.2 x Grobogan). Cross A attained the cross with the greatest number of nodes. The quantity of nodes present in soybean plants plays a crucial role in their growth as it directly impacts the potential pod development (Xu *et al.,* 2021). The number of productive nodes in this study was lower than in previous research which reached 6 to 61 nodes with an average of 27.8 (Zubaidah *et al.,* 2023bThe number of productive nodes seems to be influenced by disparities in growing seasons. The number of pods per plant (POF) ranged from 11.4 to 82.0 pods, and the highest POF was achieved by G792 from an H cross (Grobogan x UM 3.4). POF of this study was lower than previous research which reached 10 to 198 pods with an average of 80.30 pods (Zubaidah *et al.,* 2023b). The top two lines, which were associated with the highest node numbers, also exhibited a significant quantity of filled pods, with 81.60 and 75.20 pods, respectively. In contrast to the number of filled pods, soybean lines characterized by a reduced number of unfilled pods (POU) demonstrate superior performance. The lines with the lowest POU were achieved by G305 from a Q cross (UM 3.4 x Panderman), G336 from an S cross (UM 4.1 x Argomulyo), and G852 from an O cross (UM 2.4 x Grobogan) with zero pods. The same case also happened to POU (Fig. 2e).

One hundred seed weight (SEW) plays a crucial role in determining the overall seed yield, as it, along with the pod count, directly impacts the final yield of seeds. The weight of 100 seeds ranged from 10.01-20.93 grams (g) with an average of 15.85 g (Fig. 2f). There were three lines with a 100 seed weight higher than 20 g per 100 seeds, namely G92 from a P cross (UM 3.2 x Grobogan), followed by G94 from an O cross (UM 2.4 x Grobogan) and G13 from a P cross (UM 3.2

x Grobogan) with 20.93, 20.21, and 20.01. SEW is controlled by multiple genes (Ikram *et al.,* 2020; Zhao *et al.,* 2019). The gene GmCYP78A10, as highlighted by Wang *et al.* (2015), is responsible for regulating seed weight, seed width, and seed thickness. The study also suggested that a lack of strong association with this gene could potentially lead to a decline in pod numbers.

Seed yield per plant was 2.06-35.032 g with a mean of 14.27 g (Fig. 2g). Four lines had seed yields higher than 30 g per plant, namely G116 from cross W (UM 6.2 x Panderman), G94 from cross O (UM 2.4 x Grobogan), G439 from cross A (Argomulyo x UM 6.3), and G340 from the cross L (Panderman x UM 4.1) with seed yields of 35,03, 32,24, 31,75, and 31,56 g per plant respectively. G94 was the line that had the largest seed size and the highest seed yield per plant. In comparison to the study conducted by Badiaradja *et al*. (2021a), the seed yield per plant (YLDP) in the present study is higher, although it remains lower than the results reported by Zubaidah *et al*. (2023b). The discrepancy between the findings of Zubaidah *et al*. (2023b) and the current study is likely due to environmental influences, given the similarity in plant materials used. Environmental factors such as plant density (Carciochi *et al.,* 2019), different soil nutrition (Nget *et al.,* 2022), and atmospheric conditions (Kumagai and Shimono, 2023) can change YLDP. The average seed yield per plot was 208.22 g with a range from 19.00-550 g (Fig. 2). Two lines had seed yields of more than 500 g per plot, namely G224 from the Y cross (UM 6.3 x Panderman) and G646 from the O cross (UM 2.4 x Grobogan) with seed yields of 550 and 530 g. Seed yield per plot (YLD) depends on SEW (Kuswantoro *et al.,* 2014) and YLDP (Toleikiene *et al.,* 2021). SEW, YLDP, and YLD graphs have similar patterns (Fig. 2f-h). Of these three traits, SEW is a component of YLDP and YLD. The correlation between these three attributes leads to seed size affecting YLDP and YLD, resulting in the creation of analogous graphs. The seed yield can be influenced by its mathematical formula, which involves multiplying the number of seeds produced from the pod by the size of the seeds. There was a variance in disease scores between the generative and vegetative stages. In the vegetative stage, the disease score ranges from 2 to 4, while in the generative stage, the scores 3 and 4 were few (Fig. 3a and b). Many soybean lines did not receive a score of 4, implying that as the plants aged, there was a significant recovery in their overall condition. Zubaidah and Kuswantoro (2016) also reported the recovery of the soybean which was attacked by CpMMV. This is in line with the report by Malavika *et al.,* (2023), which states that the mechanism of resistance to viral infections involves the production of small-interfering RNAs (siRNAs) and other defense responses, which cause recovery symptoms. Ten lines had high disease scores in the generative stage, namely lines G240, G466, G299, G469, G407, G298, G470, G426, G297, and G48. It suggests that there is no recovery in these lines.

Principal components analysis creates new variables known as principal components, which are independent or uncorrelated and arranged based on their variance or eigenvalues (Kherif and Latypova, 2020). The principal elements capture the most significant sources of diversity within the dataset. This tool facilitates the selection of superior soybean lines by decreasing the number of traits taken into account. Across all quadrants, the F6

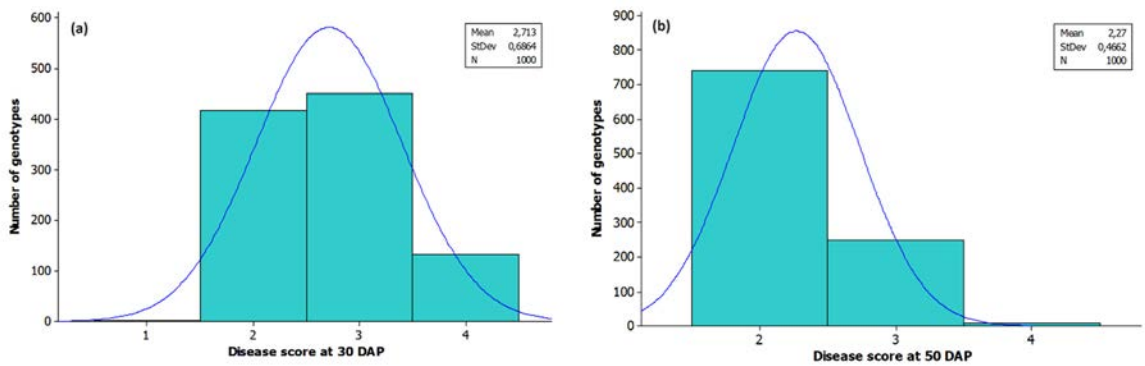


Fig. 3: Disease scores of 1000 soybean lines originated from various crosses

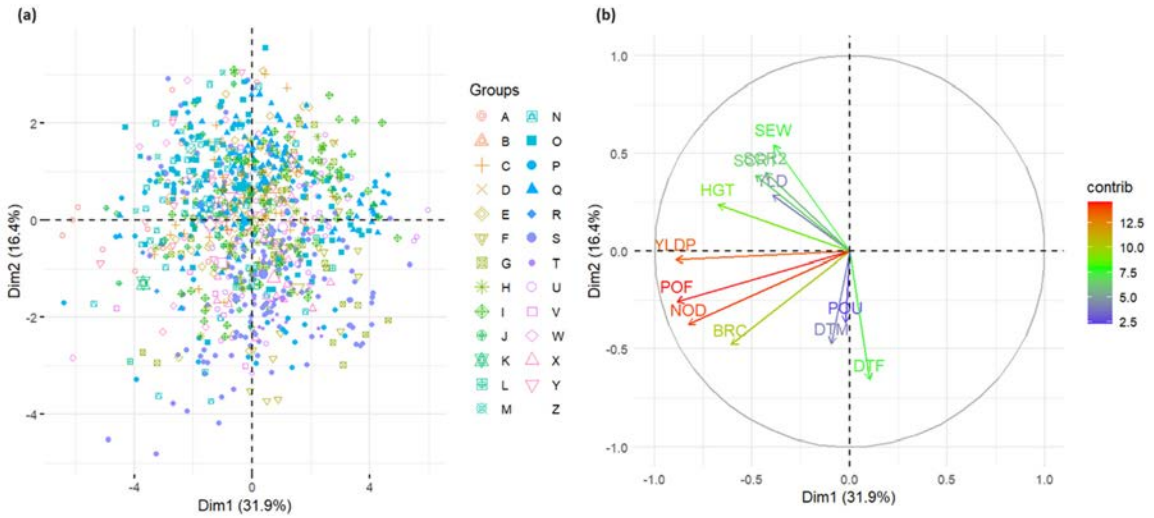


Fig. 4: Distribution of lines (a) and contribution of traits (b) of 1000 soybean lines originating from various crosses

lines were evenly dispersed, with a notable increase in the number of lines towards the center of each quadrant rather than the peripheries. Quadrant is a quarter of an area. Quadrant I is located at the top right, quadrant II is located at the top left, quadrant III is located at the bottom left, and quadrant IV is located at the bottom right of an area. Many crossings were located in quadrants I, II, and III. Quadrant I was occupied by crosses C, D, E, G, H, I, J, P, Q, S, U, Y, and Z, with crosses Q and U being more dominant in this quadrant than in others (Fig. 4a). Quadrant II was occupied by crosses A, C, E, I, J, M, N, O, P, Q, R, S, V, W, and Y, with crosses J, N, O, Q, W, and Y being more dominant in this quadrant than in others. Quadrant III was occupied by crosses A, E, G, H, I, J, K, L, N, P, Q, S, U, V, W, and Y, with cross S being dominant in this quadrant. Quadrant IV had fewer crosses, namely F, G, I, L, O, P, S, T, U, and X, with crosses G and S being dominant in quadrant IV. All of the traits are located in quadrants II and III, except DTF that located in quadrant IV. Traits that made significant contributions were POF, NOD, and YLDP. The three characteristics were situated in quadrant III, which was additionally impacted by the branch count (BRC). Quadrant II was influenced by SEW and HGT, as well as by disease score at 30 days after planting (SCR1) and disease score at 50 days after planting (SCR2). There were no traits located in quadrant I (Fig. 4b). Diverse agronomic traits play a crucial role in plant breeding initiatives, allowing for the development of cultivars that exhibit exceptional agronomic characteristics and resilience against both biotic and abiotic pressures. PCA biplot shows that lines originating from different crosses occupied different quadrants. Variations in agronomic traits and disease resistance scores among the tested lines led to differences in the positioning of these lines. The differences in line positions in this study are different from previous studies on Filial 3 (F3) (Badiaradja *et al.,* 2021b) and F5 (Zubaidah *et al.,* 2023b). The difference between Filial 4 (F4) and Filial 5 (F5) is believed to be influenced by both genetics and environmental factors, whereas the difference between F5 and F6 is more likely due to environmental factors. The reason for this is that the plants remain heterozygous in the F3 generation while approaching homozygosity in the F5 and F6 generations. In PCA biplots with smaller populations that are different from the overall population, differences occur due to differences in the populations used to establish PCA biplots (Zubaidah *et al.,* 2023b). In detail, based on the five crosses A-E, it was observed that cross A was distributed across quadrants I-III, with the majority in quadrant II, whereas cross B scattering across quadrants II and IV, with the most lines in quadrant IV. Cross C was predominantly located in quadrants I and IV, with some presence in quadrants II and III, although

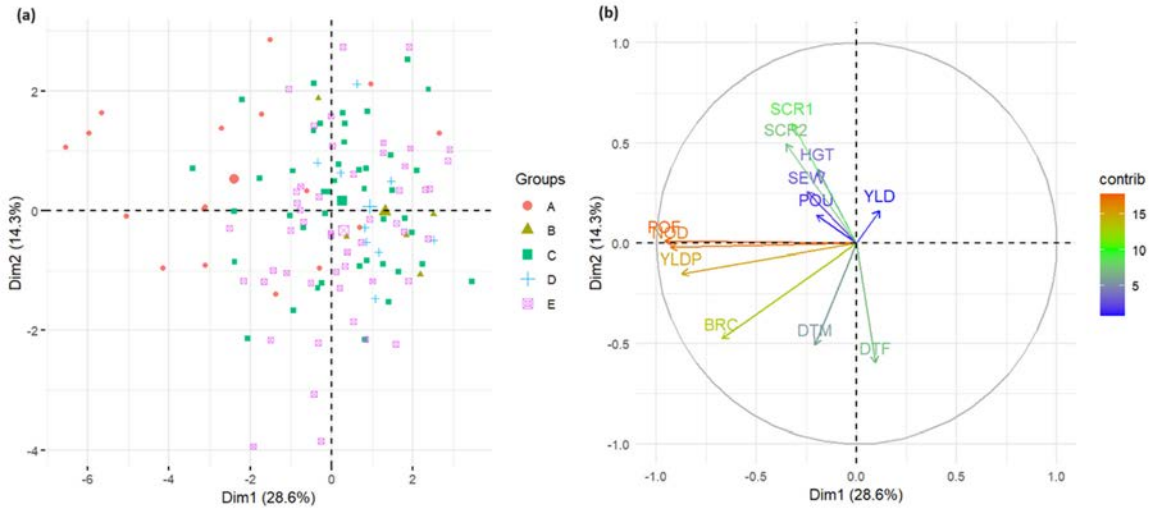


Fig. 5: Distribution of lines (a) and contribution of traits (b) of A-E crosses

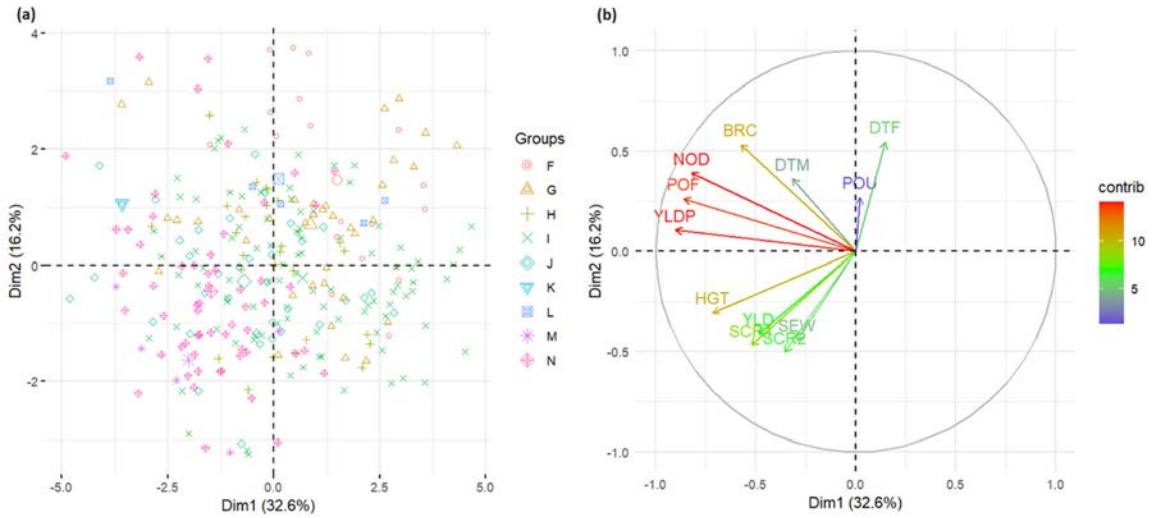


Fig. 6: Distribution of lines (a) and contribution of traits (b) of F-N crosses

in lesser quantities. Cross D was also prevalent in quadrants I and III, with only one in quadrant II. Cross E was widely distributed in quadrants I, III, and IV, but had fewer in quadrant II (Fig. 5a). The distribution pattern of all crosses closely resembled this particular pattern (Fig. 4a). Similar to the distribution of lines, the contribution of traits in crosses A-E (Fig. 5b) also resembled the contribution of traits in all crosses (Fig. 4b), with POF, NOD, and YLDP being the traits with the highest contributions. Various characteristics exhibited comparable placements, albeit with varying orientations and degrees. The key distinction was the relocation of YLD from quadrant II to quadrant I.

In the population of crosses F-N, cross F was mostly found in quadrants I and IV, but was scarce in quadrant II and absent in quadrant III. Cross G was dominant in quadrants 1, 2, and 3, with just a single occurrence in quadrant III. Crosses H, I, and J were evenly distributed across all four quadrants. Cross K was in quadrant II, cross L in quadrants I and II, and cross M in quadrant III. Cross N was

predominantly located in quadrant III, although it could also be observed in the remaining three quadrants (Fig. 6a). In all nine crosses, cross G was evenly distributed across all four quadrants, while cross K was specifically located in quadrant III. Cross L was in quadrants III and IV, cross M in quadrant II, and cross N was mainly spread in quadrant II, although it was also found in other quadrants (Fig. 4b). The highest trait contribution was achieved by YLDP, POF, and NOD. The contribution of traits had a similar arrangement to all lines, only the arrangement was reversed, where YLDP, POF, and NOD were in quadrant II (Fig. 6b) previously in quadrant III (Fig. 4b). Similarly, other attributes were noted with slightly varying levels of significance. The population of O-T crosses shows that O-cross was mostly distributed in quadrant II followed by quadrant I. O cross was also found in quadrants III and IV, although only a few. The P cross showed an equal distribution among the four quadrants. Q cross was scattered around quadrant I and quadrant II, and a few in quadrant III. R cross was in quadrants II and III. S cross was in quadrants IV and III followed by I and II. T cross was in quadrant IV (Fig. 7a). These six crosses (O-T) were very similar to all crosses (Fig. 4a). Traits made a significant impact on the entire crossbreeding process, with YLDP, POF, and NOD being the primary contributors and other traits serving as subsequent supporters. A minor difference existed in the case of POU and DTM, which had moved from quadrant III (Fig. 4b) to quadrant IV (Fig. 7b).

In the U-Z crosses, it was found that cross U was distributed in quadrants III and IV, while crosses V was in quadrant I. Cross W was distributed between quadrants I and IV, with a small representation in quadrant II. Cross X was distributed in quadrants II and III. Cross W was distributed between quadrants I and IV, with a small representation in quadrant II. Cross Z was distributed across quadrant II and quadrant I, with a minor presence in the adjacent quadrants (Fig. 8a). In the overall population, cross U primarily occurred in quadrant I, followed by quadrants III and IV, with minimal representation in quadrant II. The distribution of Cross V was primarily in quadrants III and II, with a lesser occurrence in quadrant IV. Crosses W spanned quadrants II and III, with slight representation in other quadrants. Cross X had a predominant presence in quadrant IV while exhibiting minimal presence in quadrant III. Cross Y was located in quadrant II, with minimal presence in quadrants I and III, and two markings in quadrant IV. Cross Z was primarily in quadrant I, with minor representation in other quadrants (Fig. 4a). Variances in line placements are evident when population division is carried out. Similar to the line distribution, the contribution of traits in the U-Z population also differed from the total A-Z population. In the A-Z population, all trait contributions were located in quadrants I and IV (Fig.

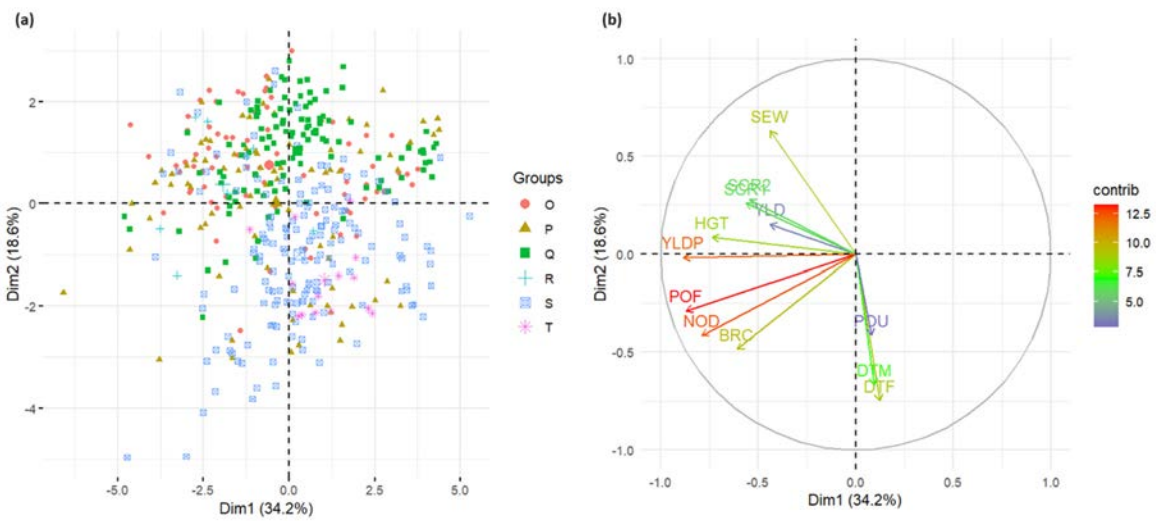


Fig. 7: Distribution of lines (a) and contribution of traits (b) of O-T crosses

Table 1: Traits correlation of 1000 soybean lines originated from different crosses

Traits	YLD	SCR1	SCR2	YLDP	SEW	POU	POF	NOD	BRC	HGT	DTM
SCR1	0.200**										
SCR2	0.118**	0.684**									
YLDP	0.241**	0.286**	0.277**								
SEW	0.140**	0.208**	0.188**	0.406**							
POU	-0.090**	-0.100**	-0.114**	0.008	-0.097**						
POF	0.180**	0.27**	0.211**	0.807**	0.221**	0.099**					
NOD	0.130**	0.201**	0.150**	0.721**	0.143**	0.175**	0.900**				
BRC	0.121**	0.058	0.048	0.514**	-0.032	0.039	0.585**	0.6**			
HGT	0.530**	0.309**	0.263**	0.529**	0.276**	-0.038	0.436**	0.379**	0.252**		
DTM	-0.027	0.048	0.046	0.116**	-0.148	0.022	0.093**	0.123**	0.118**	-0.038	
DTF	-0.104**	-0.047	-0.077**	-0.147**	-0.415**	0.092**	-0.025	0.052	0.176**	-0.101**	0.393**

** = significant at $\alpha_{0.05}$; YLD = seed yield per plot, YLDP = weight of seeds per plant, SEW = weight of 100 seeds, NOD = number of productive nodes, POF = number of filled pods, POU = number of unfilled pods, BRC = number of branches, HGT = plant height, DTF = days to maturity, DTF = days to flowering, SCR1 = disease score at 30 days after planting, SCR2 = disease score at 50 days after planting.

8b), whereas the all population was predominantly in quadrants II and III, except for DTF, which was in quadrant IV (Fig. 4b). The direction of the arrow in a PCA biplot signifies the impact of a trait's position, with the length of the arrow representing the extent of that trait's influence. If an arrow points towards quadrant I, genotypes located close to this direction within quadrant I exhibit higher values for that specific trait. The length of the arrow is a reflection of its importance when compared to other attributes. This study findings indicated that YLDP, POF, and NOD made similar and equally significant contributions, whereas the disease score exhibited a wider angle and relatively shorter arrow than the three traits (Fig. 4b). YLDP, POF, and NOD play a crucial role in population diversity, as indicated by the long arrows. A disease score with a relatively shorter arrow suggests that the impact of the disease score on the diversity of this population is minimal. The direction of the YLDP, POF, and NOD arrows in the same direction shows that these three traits contribute to each other, while the disease score with a larger angle does not support the three traits. Zubaidah *et al*. (2023b) with the same cross as this study also reported that YLDP, POF, and NOD had unidirectional contributions. Badiaraja *et al*. (2021b) reported that in the F3 of the Grobogan x UM 6.1 cross, seed yield per plant and seed number contributed in the same direction, while the contribution of other characters varied. In different crosses, unidirectional contributions from NOD, FOP, POU, and YLDP were also reported by Kuswantoro *et al*. (2020). In smaller populations, YLDP, POF, and NOD also made the largest contributions. The contribution direction of the U-Z population from YLDP, POF, and NOD is opposite to that of the A-E, F-N, and O-T populations. This means that the U-Z population has different characteristics from the other three populations. Changes in traits within subpopulations are a result of variations among populations (Zubaidah *et al.,* 2023b).

All observed agronomic traits were significantly correlated except SEW with BRC, DTF with NOD and POF, and POU with DTM, HGT, BRC, and YLDP. Disease score traits also correlate with agronomic traits except for SCR1 with DTM, DTF, and BRC, as well as SCR2 BRC, and DTM (Table 1). Negative correlations were found between DTF and SEW, YLDP, and YLD, DTM with SEW, and POU with SEW and YLD. The negative correlation of disease score traits was obtained in SCR1 with POU, and SCR2 with DTF and POU. Sutrawati *et al*. (2021) reported a negative correlation between CpMMV infection and with number of seeds and pods. It means that CpMMV disease-induced biotic environmental stress reduces both DTF and POU. In the study by Jeger (2020), it was noted that the tolerance to virus diseases is influenced by the duration and timing of the reproductive period, as well as the allocation of resources from growth to reproduction. Rapidly developing cultivars can surpass the virus, ensuring consistently high yields despite potential initial infection. Synchrony in flowering and pod formation can influence the timing of susceptibility. Cultivars with abbreviated blooming cycles could limit the timeframe for viral spread (McGarry *et al.,* 2017).

Unlike the overall population, subpopulation A-E showed a lack of correlation among many

traits. The trait with the most correlation was POF, where POF correlated with other agronomic traits except DTM, DTF, and YLD. In terms of biotic environmental stress, the disease score did not

Table 2: Traits correlation of subpopulation

Traits	YLD	SCR1	SCR2	YLDP	SEW	POU	POF	NOD	BRC	HGT	DTM
A-E- crosses											
SCR1	0.03										
SCR2	-0.077	0.652**									
YLDP	-0.1	0.09	0.128								
SEW	-0.051	0.06	-0.027	0.321**							
POU	0.098	-0.041	-0.026	0.03	-0.076						
POF	-0.106	0.241**	0.258**	0.814**	0.204*	0.221*					
NOD	-0.104	0.207*	0.219*	0.755**	0.166	0.311**	0.938**				
BRC	-0.061	-0.005	0.042	0.577**	-0.057	0.036	0.597**	0.576**			
HGT	0.286**	0.16	0.136	0.14	0.036	0.141	0.186*	0.161	-0.089		
DTM	0.022	0.046	0.142	0.231	-0.078	-0.183*	0.102	0.099	0.237**	-0.065	
DTF	0.006	-0.114	-0.083	-0.092	-0.249**	-0.038	-0.129	-0.093	0.156	0.048	0.409**
F-N crosses											
SCR1	0.334**										
SCR2	0.232**	0.667**									
YLDP	0.280**	0.334**	0.191**								
SEW	0.135**	0.139**	0.061	0.326**							
POU	-0.092	-0.064	-0.117	0.012	-0.02						
POF	0.226**	0.299**	0.107**	0.817**	0.157**	-0.009					
NOD	0.171**	0.208**	0.069	0.778**	0.103	0.098	0.873**				
BRC	0.084*	0.021	-0.022	0.529**	-0.006	0.036	0.541**	0.592**			
HGT	0.585**	0.379**	0.290**	0.586**	0.267**	-0.065	0.437**	0.389**	0.201**		
DTM	0.116	0.182**	0.098	0.217**	-0.196**	0.044	0.193**	0.254**	0.250**	0.182**	
DTF	-0.172	-0.085	-0.038	-0.163**	-0.408**	0.049	-0.08	-0.010	0.128*	-0.161**	0.323**
O-T crosses											
SCR1	0.214**										
SCR2	0.128**	0.721**									
YLDP	0.292**	0.334**	0.378**								
SEW	0.157**	0.247**	0.254**	0.445**							
POU	-0.141**	-0.132**	-0.143**	-0.022	-0.178**						
POF	0.218**	0.314**	0.299**	0.803**	0.238**	0.056					
NOD	0.155**	0.258**	0.223**	0.681**	0.129**	0.118*	0.903**				
BRC	0.190**	0.120*	0.110*	0.512**	-0.046	0.001	0.618**	0.634**			
HGT	0.531**	0.375**	0.337**	0.600**	0.306**	-0.06	0.502**	0.427**	0.323**		
DTM	-0.085	-0.120*	-0.092	-0.046**	-0.329**	0.193**	0.035	0.104*	0.111*	-0.08	
DTF	-0.085	-0.036	-0.09	-0.179**	-0.548**	0.140**	0.015	0.112*	0.219**	-0.07	0.475**
U-Z crosses											
SCR1	0.081										
SCR2	0.024	0.641**									
YLDP	0.187*	0.229**	0.272**								
SEW	0.071*	0.361**	0.358**	0.434**							
POU	-0.093	-0.114	-0.110	0.070	-0.015						
POF	0.149**	0.107**	0.127**	0.811**	0.316**	0.277**					
NOD	0.130	0.016	0.045	0.720**	0.245**	0.306**	0.922**				
BRC	0.099**	-0.025	0.016	0.487**	-0.037	0.094	0.578**	0.547**			
HGT	0.485**	0.136	0.110	0.447**	0.120	-0.124	0.406**	0.370**	0.318**		
DTM	-0.043	0.287**	0.236**	0.324**	0.412**	-0.052	0.180**	0.152**	0.069	0.084	
DTF	-0.088	0.016	-0.108	-0.021	0.042	0.091	0.010	0.067	0.132**	-0.176*	0.521**

* = significant at $\alpha_{0.05}$, ** = significant at $\alpha_{0.01}$, YLD = seed yield per plot, YLDP = weight of seeds per plant, SEW = weight of 100 seeds, NOD = number of productive nodes, POF = number of filled pods, POU = number of unfilled pods, BRC = number of branches, HGT = plant height, DTF = days to maturity, DTF = days to flowering, SCR1 = disease score at 30 days after planting, SCR2 = disease score at 50 days after planting

exhibit any correlation with other agronomic factors, except SCR1 and SCR2 with NOD and POF (Table 2). The F-N subpopulation had many agronomic traits that correlated with each other. HGT and YLD showed the strongest correlation among agronomic traits, whereas POU did not exhibit any correlation with other agronomic traits. Disease score traits in this population also correlate with many agronomic traits, except SCR1 with DTF and POU, and SCR2 with BRC, DTM, DTF, and POU (Table 2). The O-T subpopulation displays numerous agronomic characteristics that are interconnected. The agronomic characteristic that showed the strongest correlation was NOD, with POF and YLDP following closely behind. Disease score traits in this population also correlated with many agronomic traits except SCR1 with DTF and SCR2 with DTF and DTM. HGT correlated with SCR1 and SCR2 in F-N and O-T crosses (Table 2). Different leaf arrangements and taller growth in plant varieties can change microclimates within the canopy, potentially decreasing the humidity and temperature conditions that are conducive to virus transmission by insect vectors (Jones, 2016). In the U-Z subpopulation, the correlated and uncorrelated agronomic traits were almost equal. YLDP was an agronomic trait with other traits except POU and DTF. SCR1 correlates with SEW and DTM, while SCR2 correlates with SEW and YLDP (Table 2). Understanding the relationship between agronomic traits is crucial in plant breeding, as it enables the identification of parent plants with a desirable mix of traits. The majority of agronomic traits examined in this study showed significant correlations with one another. Several studies have shown consistent findings, indicating a correlation between branch number and seed yield per plant as well as pod number (Zhao *et al.,* 2019). Additionally, another study found a positive correlation between branch number and pod number (Xu *et al.,* 2021), while seed yield was linked to 100-seed weight in a separate study (Nataraj *et al.,* 2021). Moreover, another study reported a positive correlation between seed yield and pod number (Gawale *et al.,* 2022). This event correlation allows the selection of genotypes possessing numerous desirable traits to have a higher probability. There were no negative correlations in this study (Tables 1 and 2). This study mirrors earlier research findings, which identified correlations in certain agronomic traits without any negative correlations present (Zubaidah *et al.,* 2023b). The negative correlation of disease score trait was obtained on SCR1 with POU, and SCR2 with DTF and POU. Disease score traits also correlated with agronomic traits except SCR1 with DTM, DTF, and BRC, as well as SCR2 with BRC and DTM (Tables 1 and 2).

According to Zubaidah *et al*. (2023a), there were notable variations in agronomic traits between resistant and susceptible genotypes, particularly in terms of seeds per plant, total pods, and filled pods number. Notably, five susceptible genotypes exhibited poorer performance compared to five resistant genotypes. The study revealed that there was a direct correlation between seed yield per unit area and seed yield per plant with the disease score. This is likely because the soybean lines had a tolerance mechanism rather than a resistance mechanism. As plants age, resistant and tolerant genotypes may undergo recovery from virus infections (Zubaidah and Kuswantoro, 2016). Resistant varieties may experience virus infections with minimal impact on yield, while tolerant varieties may face higher infection rates yet still achieve optimal yield (Sutrisno and Kuswantoro, 2016; Eid *et al.,* 2023). van den Berg *et al.* (2017) also reported the existence of a tolerance mechanism that can provide better results for comparable disease severity. This is in accordance with McCarville and Ayres (2018) that host health increases while providing pathogen fitness. In environmental biotic stress, small RNAs (sRNAs) perform a crucial role in plant immunity by leveraging the RNA silencing machinery (Huang *et al.,* 2016). The role of hormones in regulating plant responses to disease is a contributing factor to disease tolerance in plants (Alazem and Lin, 2015). Agronomic conditions influence plant and disease interactions, including ontogenic resistance by changing the length of the growth period and modifying the development of invaders through microclimate and food sources (Haider *et al.,* 2017). Rapidly developing cultivars can surpass the virus, ensuring consistently high yields despite potential initial infection. Synchrony in flowering and pod formation can influence the timing of susceptibility. Varieties with shorter flowering periods may reduce the opportunity for viral transmission (McGarry *et al.,* 2017). The variety of agronomic traits found in

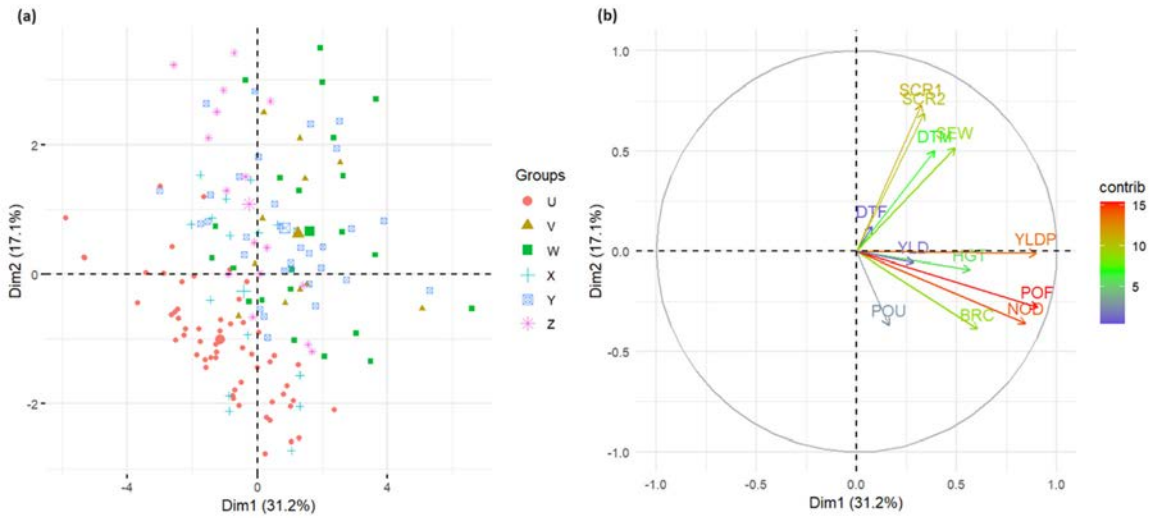


Fig. 8: Distribution of lines (a) and contribution of traits (b) of U-Z crosses

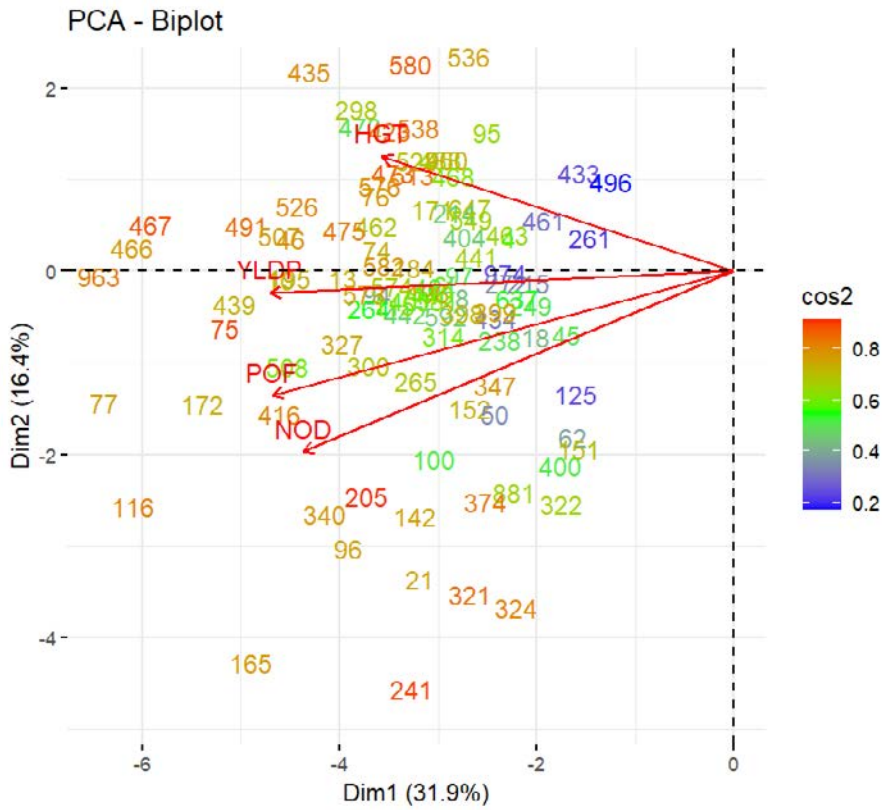


Fig. 9: One hundred soybean lines selected based on the three highest contribution traits

soybean populations plays a crucial role in boosting crop resilience to viral diseases. This is achieved through effective hormonal regulation, which can strengthen systemic acquired resistance and offer a wider range of protection against viral infections (Kamaal *et al.,* 2023).

The principal components accurately represent the majority of the variance observed in the total variance of the original variables (Greenacre *et al.,* 2022). This tool can be used to decrease the traits for selecting a superior variety. Based on the traits with consistent contributions and correlations, namely YLDP, POF, NOD, and HGT, 100 lines were selected. These 100 lines were located in quadrants III and II, matching the characteristics' impacts also found in quadrant III (Fig. 9). From these 100 lines, the five best lines based on the three traits were G77, G963, G116, G172, and G165, while the five least favorable lines among the 100 lines were G261, G536, G468, G549, and G125. Among all the traits, the five most outstanding lines displayed colors that transitioned from red to orange, in contrast to the five less desirable lines which featured shades from green to blue. The red to orange colors indicate that, besides being influenced by YLDP, POF, NOD, and HGT, these lines are also influenced by other traits, whereas the green to blue colors suggest that the other traits play a lesser role in these five lines.

Direct selection on YLD was not feasible as it was positively correlated with disease scores in the entire population and subpopulations. Consequently, selecting for high YLD could lead to a high disease score. In general, indirect selection is carried out based on correlation (Casagrande *et al.,* 2022), but not all correlations can be used for direct selection (Conte *et al.,* 2020). Selection was carried out based on traits with high contribution and correlation, namely YLDP, NOD, POF, and HGT. Berhanu *et al*. (2021) identified a meaningful link between seed yield and the quantity of filled pod nodes. The importance of plant height in selection for high yields was also pointed out by Lü *et al*. (2016). Bhor *et al*. (2014) recommended using plant height as a selection criterion, in addition to considering factors like the weight of 100 seeds and the number of pods when choosing superior varieties. In previous research (Zubaidah *et al.,* 2023b), no correlation was found with disease score so it was suspected that there was a tolerance and resistance mechanism. In this study, disease score and YLD had a positive correlation so the tolerance mechanism was more appropriate than the resistance mechanism. The tolerance mechanism enhances the well-being of the host while exerting a neutral to beneficial impact on the fitness of the pathogen (McCarville and Ayres, 2018). The conclusions drawn from this study have practical implications for the enhancement of soybean breeding programs to increase resistance against Cowpea mild mottle virus. This can be accomplished by developing polygenic resistance through the inclusion of multiple resistance genes in soybean varieties, leading to a more comprehensive and enduring defense (Karasov *et al.,* 2020). Furthermore, the incorporation of various resistance traits can be facilitated by utilizing diverse germplasm. Diverse genetic backgrounds can provide distinct resistance mechanisms and enhance the overall resilience of crops (Nelson *et al.,* 2018).

CONCLUSION

Agronomic traits and biotic environmental stress, such as virus disease, have a notable impact on soybean seed yield, with a wide range of diversity seen in tested lines. The lines tested showed diversity in agronomic and disease score traits. The breadth of diversity is evident in the wide spectrum of measured values for each agronomic attribute, along with disease scores spanning from 1 to 4. Four lines with seed yields higher than 30 g per plant, G116, G94, G439, and G340 exhibited the highest agronomic value. According to the PCA biplot, the traits contributing most significantly were number of productive nodes per plant, the number of filled pods per plant, and seed yield per plant. The most significant factors that influenced the four subgroups were these three traits. In three subpopulations as well as the overall population, YLD had a minimal contribution. SCR1 and SCR2 contributed medium to the total population and subpopulation, except for the U-Z subpopulation, which contributed quite highly. Substantial correlations were found among the various agronomic traits studied, except for SEW and BRC, DTF and POF, and POU and DTM, HGT, BRC, and YLDP. The trait with the most correlation was POF, where POF correlated with other agronomic traits except DTM, DTF, and YLD. The four subpopulations' correlations differed greatly from one another: many

traits in the A-E subpopulation were uncorrelated, many agronomic traits were correlated in the F-N and O-T subpopulations, and the correlated and uncorrelated agronomic traits were nearly equal in the U-Z subpopulation. A strong correlation was consistently observed between plant height and seed yield. Seed yield per plant had a positive correlation with disease score, making it unsuitable as a selection criterion. This positive correlation indicates a tolerance mechanism, allowing soybeans to produce high seed yields even when infected with CpMMV. Seed yield per plant, filled pod number, node number, and plant height were appropriate to select 100 superior soybean lines. The 100 soybean varieties present a hopeful opportunity to decrease dependence on pesticides, ultimately protecting the environment and promoting sustainable farming practices.

AUTHOR CONTRIBUTIONS

H. Kuswantoro provided the genetic material, designed the research, analyzed the data, interpreted the results, wrote the draft manuscript, and revised the final manuscript; S. Zubaidah provided the study idea, designed the research, interpreted the results, wrote the draft manuscript, and revised the final manuscript; E. Uge designed the research, collected data, and wrote the draft manuscript; K. Rozana performed the literature review, wrote the draft manuscript, and revised the final manuscript; Purwantoro collected data, performed the literature review, and revised the final manuscript; J. Purnomo performed the literature review, wrote the draft manuscript, and revised the final manuscript.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest regarding the publication of this manuscript. The ethical issues, including plagiarism, informed consent, misconduct, data fabrication and/or falsification, double publication and/or submission, and redundancy, were observed by the authors.

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ABBREVIATIONS

BRC	the number of branches per plant
cm	Centi meter
CpMMV	Cowpea mild mottle virus
DAP	Days after planting
Dim1	Dimension 1
Dim2	Dimension 2
DTF	days to flowering
DTM	days to maturity
et al	And others
F3	Filial 3
F4	Filial 4
F5	Filial 5
F6	Filial 6

Fig.	Figure
g	Gram
ha	Hectare
HGT	Plant height
KCl	Kalium chloride
kg	Kilogram
kg/ha	Kilogram per hectare
kg urea/ha	kg urea per hectare
m	Meter
MS Excel	Microsoft Excel
NOD	Number of productive nodes per plant
PCA	Principal component analysis
PCA-biplot	Principal component analysis biplot
POF	Number of filled pods per plant
POU	Number of unfilled pods per plant
SCR1	Disease score at 30 days after planting
SCR2	Disease score at 50 days after planting
SEW	100-seed weight
sRNAs	Small RNAs
siRNAs	Small-interfering RNAs
SP-36	Superphosphate 36
YLD	Seed yield per plot
YLDP	Seed yield per plant

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AUTHOR (S) BIOSKETCHES

Kuswantoro, H., Dr., Principal Researcher, Research Center for Food Crops, Research Organization for Agriculture and Food, National Research and Innovation Agency (BRIN), Jl. Raya Jakarta-Bogor Km 46, Bogor 16911, West Java, Indonesia.
- Email: *heru032@brin.go.id; herukusw@gmail.com*
- ORCID: 0000-0001-9241-0573
- Web of Science ResearcherID: FZL-6363-2022
- Scopus Author ID: 53866614600
- Homepage: https://brin.go.id/orpp/pusat-riset-tanaman-pangan/page/personil-sumberdaya-manusia

Zubaidah, S., Dr., Professor, Department of Biology, Faculty of Mathematics and Natural Sciences, State University of Malang, Jl. Semarang 5 Malang 65145, East Java, Indonesia.
- Email: *siti.zubaidah.fmipa@um.ac.id*
- ORCID: 0000-0002-0718-6392
- Web of Science ResearcherID: AFR-6302-2022
- Scopus Author ID: 57216572363
- Homepage: http://biologi.fmipa.um.ac.id/dosen-jurusan-biologi/dosen-s3-pendidikan-biologi/

Uge, E., M.Sc., Junior Researcher, Research Center for Food Crops, Research Organization for Agriculture and Food, National Research and Innovation Agency (BRIN), Jl. Raya Jakarta-Bogor Km 46, Bogor 16911, West Java, Indonesia.
- Email: *emer002@brin.go.id*
- ORCID: 0000-0002-0912-7599
- Web of Science ResearcherID: NA
- Scopus Author ID: 58682812700
- Homepage: https://brin.go.id/orpp/pusat-riset-tanaman-pangan/page/personil-sumberdaya-manusia

Rozana, K., M.Si, Biotechnology Lecturer, Department of Biology, Faculty of Mathematics and Natural Sciences, State University of Malang, Jl. Semarang 5, Malang, East Java, Indonesia.
- Email: *kennis.rozana.fmipa@um.ac.id*
- ORCID: 0000-0001-9503-7890
- Web of Science ResearcherID: AAZ-7043-2021
- Scopus Author ID: 57219400437
- Homepage: http://biologi.fmipa.um.ac.id/team/kennis-rozana-s-pd-m-si/ http://bioteknologi.fmipa.um.ac.id/kennis-rozana-s-pd-m-si/

Purwantoro, B.Sc., Senior Researcher, Research Center for Food Crops, Research Organization for Agriculture and Food, National Research and Innovation Agency (BRIN), Jl. Raya Jakarta-Bogor Km 46, Bogor 16911, West Java, Indonesia.
- Email: *purwantorosp@gmail.com*
- ORCID: 0000-0002-1644-7064
- Web of Science ResearcherID: DNK-7780-2022
- Scopus Author ID: 57191892605
- Homepage: https://brin.go.id/orpp/pusat-riset-tanaman-pangan/page/personil-sumberdaya-manusia

Purnomo, J., M.Sc., Principal Researcher, Research Center for Food Crops, Research Organization for Agriculture and Food, National Research and Innovation Agency (BRIN), Jl. Raya Jakarta-Bogor Km 46, Bogor 16911, West Java, Indonesia.
- Email: *jokop9775@gmail.com*
- ORCID: 0000-0003-1187-1402
- Web of Science ResearcherID: NA
- Scopus Author ID: 57871797900
- Homepage: https://brin.go.id/orpp/pusat-riset-tanaman-pangan/page/personil-sumberdaya-manusia

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