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Research Article

Understanding gene interactions controlling resistance to pepper yellow leaf curl disease through phenotype-based analysis

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ABSTRACT

Pepper yellow leaf curl disease (PYLCD) is the primary disease that affects chili plants, resulting in a loss of quality and quantity. The identification of chili plants resistant to PYLCD is a solution to support optimal chili cultivation. The purpose of this study was to estimate genetic parameters to obtain information on the genetic control of chili resistance to PYLCD. The genotypes used in this study consisted of four parental, four hybrid genotypes, and 180 individuals of the F_2 population. The results showed that the genotypes "F6074" and "IPBC12" were categorized as resistant, while the genotypes "IPBC5" and "YUNI" were categorized as susceptible. The distribution of resistance level in chili peppers to yellow curly leaf disease tends to follow a ratio of 13:3, with a dominance of susceptible traits. The assumption for this phenomenon is that resistance to PYLCD is controlled by at least two genes. Both genes have dominant and recessive epistatic interactions.

Keywords: *Begomovirus*; chi-square; epistasis; resilience

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INTRODUCTION

Pepper yellow leaf curl disease (PYLCD) is a major disease of chili peppers caused by Pepper yellow leaf curl virus/PYLCV (Begomovirus; Geminiviridae). The virus has been reported to cause considerable damage and yield loss (Sharma & Kumar, 2017). Yellow curly leaf disease is also known to affect several other commodities, including tomatoes (Koeda et al., 2020), eggplants (Putri et al., 2023; Soro et al., 2021), cassava (Dye et al., 2023), and beans (Ramesh et al., 2019). Symptoms of a typical yellow curly leaf disease attack are generally easy to recognize. The symptoms include chlorosis, causing yellowing of leaves, cupping of leaf margins, leaf curling, and advanced symptoms, such as flower drop and stunted plants (Pandey et al., 2021; Sidik et al., 2023).

Chili plants that are resistant to PYLCD have been widely developed in Indonesia. However, to date, few reported chili genotypes have been resistant to PYLCD. There are several reasons for the difficulty in assembling chili genotypes resistant to PYLCD, one of which is the potential changes that occur in PYLCV. Chili plants have the potential to simultaneously experience mixed infections from several viral species (Annisaa et al.,

2021). Mixed infection of several types of Begomovirus in one plant can cause an increase in the level of symptoms that are more severe than a single virus infection (Singh et al., 2016), and recombination or pseudo-recombination events can trigger the occurrence of new virus strains (García-Cano et al., 2006; Mohamed, 2010). These conditions can lead to a breakdown of plant resistance (Rubio et al., 2020; Singh et al., 2016).

In addition to the evolutionary changes occurring within the pathogen, the lack of information regarding resistance genes and markers, as well as the inheritance patterns of resistance to PYLCV in chili peppers, presents a significant challenge in the development of resistant varieties (Siddique et al., 2022). Despite the extensive diversity of species and varieties within chili peppers, this remains a complex issue. Some researchers have documented that chili peppers of the same variety can exhibit varied resistance responses when subjected to pathogen attacks (Sayekti et al., 2021; Siddique et al., 2022; Suwor et al., 2021). Consequently, it is imperative to estimate genetic parameters as the basis for investigating the inheritance of chili resistance to yellow leaf curl disease.

Estimating genetic parameters involves quantifying genetic properties that explain genetic control over traits (Hansen et al., 2024). Estimating genetic parameters through a qualitative approach involves categorising traits that exhibit distinct classes or categories, such as resistant vs. susceptible, rather than continuous measurements. This approach analyses inheritance patterns by scoring phenotypes into discrete groups and using methods like segregation analysis to infer genetic control, dominance relationships, and gene action involved in a trait. The purpose of this study was to estimate genetic parameters to obtain information on the genetic control of chili resistance to PYLCD. In this study, the estimation of genetic parameters was conducted to acquire information on the genetic mechanisms governing chili resistance to this disease.

MATERIALS AND METHODS

Study area and plant materials

This research was conducted at IPB University Teaching Farm, from June to December 2023. The site is located at IPB Darmaga Campus, Cikabayan Bawah, Babakan Village, Bogor, Indonesia (250 m above sea level (m asl)).

At first, two genotypes of chili pepper (IPBC12 and IPBC5) were planted in an insect-free greenhouse at an altitude of 250 m asl as parents. The female parent (IPBC12) is a chilli genotype resistant to PYLCD, while the male parent (IPBC5) is susceptible. The first progeny (F_1 generation) from the cross between the two parents was planted and left to self-pollinate for harvesting as the F_2 generation (F2.012005). In this study, two parental genotypes (IPBC12 and IPBC5), F_1 generation (F1.012005), and 180 individuals of the F_2 generation (F2.012005) were used as genetic materials.

Experimental procedure

Plant resistance testing was conducted in several steps, including preparing virus inoculum and vector insects, plant preparation, virus inoculation, and symptom observation. The vector used was the whitefly (*Bemisia tabaci*), sourced from eggplant and chili plantations in the IPB Dramaga area. The collected whitefly imagos were reared and allowed to breed in insect boxes for 1 to 2 months before use. Healthy cotton (*Gossypium hirsutum*) plants served as the hosts for the whiteflies. The inoculum was the *Pepper yellow leaf curl virus* (PYLCV) isolate obtained from the Plant Virology Laboratory, Department of Plant Protection, IPB University.

Plant preparation was carried out by sowing the test genotypes in seedling trays for 21 days or until the plants developed two true leaves. The 21-day-old seedlings were then transplanted into individual pots for subsequent inoculation. The planting medium used was a mixture of soil, compost, and cocopeat. During the seedling stage, maintenance included daily watering and fertilisation twice a week. Virus inoculation was carried out using the individual inoculation method proposed by Ganefianti et al. (2015) and Gaswanto et al. (2016).

A total of 20 parental plants, 20 F_1 generation plants, and 180 F_2 individuals were tested and observed over approximately 60 days. Observations focused on plant resistance characteristics, including the incubation period, disease incidence, and severity. The Incubation period is when the first symptoms appear following inoculation. Plants were observed daily until symptoms of PYLCD infection became visible (observations were conducted up to 30 days after inoculation/DAI). Disease incidence was assessed by calculating the number of plants exhibiting symptoms relative to the total number of plants in the tested population. Disease severity was assessed based on the symptoms observed on the plant leaves, with scores assigned on a scale from 0 to 4 (Table 1).

Table 1. Criteria for *Begomovirus* infection symptoms to determine disease severity scores.

Skor	Symptom
0	Healthy plant (no symptoms)
1	Yellow leaves
2	Yellow and curly leaves
3	Yellow curly leaves and cupping (upward and downward)
4	Yellow curly leaves and cupping (upward and downward), stunted plant

Data analysis

In this study, a ratio comparison of data distribution was conducted using the Chi-square (χ^2) test. The Chi-square (χ^2) value was calculated using the following formula:

$$\chi^2 = \sum \left(\frac{(O - E)^2}{E} \right)$$

Notes:
χ^2 = Chi-square value
O = Observed frequency
E = Expected frequency

The segregation ratio of plant resistance levels was used to estimate the genetic model of plant resistance to PYLCD quantitatively. The genetic model was determined using the phenotypic ratio, controlled by major genes in F_2 segregating populations, as stated by Burns (1976). Normality test was performed using Minitab 16 software, while data compilation and Chi-square analysis were conducted with the assistance of Microsoft Excel 365.

RESULTS AND DISCUSSION

Three characteristics related to the resistance response of chili plants to PYLCD were observed: the incubation period, the incidence rate, and disease severity. Observations were conducted on parental populations, hybrids (F_1 populations), and F_2 populations. Disease severity was determined using scores for observed symptoms. The scoring was based on the types of symptoms shown in Figure 1.

Based on these results (Table 2), recessive alleles are suspected to control plant resistance, so resistant traits tend to be recessive to susceptible traits. Traits controlled by a recessive gene will only appear when an individual has a pair of recessive alleles and will be covered if the individual is in a heterozygous condition. In this case, the F_1 population will have a heterozygous genetic constitution, so the traits that appear tend to be dominant, while recessive traits are not observed in this population.

Figure 1. Symptom score/level of chilli plants due to *Pepper yellow leaf curl disease*. 0 = healthy plants (no symptom); 1 = yellow leaves; 2 = yellow and curly leaves; 3 = Yellow curly leaves and cupping (upward and downward).

Table 2. Variables related to resistance of chilli plants to *Begomovirus* attack.

Variable	Genotype		
	IPBC12	IPBC5	F_1(012 x 005)
Incubation periods (DAI[1])	11-30	7-13	3-11
Disease incidence (%)	60.00	100.00	100.00
Disease severity (%)	19.00	76.00	76.25

[1] DAI = day after inoculation.

The distribution of PYLCD symptom scores/types in the F_2 population derived from the IPBC12 × IPBC5 cross was not normally distributed (Figure 2). Furthermore, as the symptom scores represent categorical data, the inheritance analysis in this study was conducted using a qualitative approach.

The distribution pattern of chili resistance levels to PYLCD was studied in a cross-population between IPBC12 (female parent) and IPBC5 (male parent). The two parents used were chili genotypes that had different levels of resistance. The female parent (IPBC12) is a genotype that is included in the resistant category, while the male parent (IPBC5) is a genotype that is susceptible to yellow curly leaf disease (Ayu et al., 2021; Sayekti et al., 2021). The use of parents with different resistance levels is expected to represent different genetic constitutions related to resistance to yellow curly leaf disease. The two parents are expected to be used to study the genetics of chili resistance to virus infections through phenotype segregation.

Based on the observed symptom scores and types, chili resistance to Begomovirus exhibits a distribution in which the two parents can be clearly distinguished (Table 3). The female parent (IPBC12) is a genotype classified as mildly resistant, with symptom scores ranging from 0 to 2. In contrast, the male parent (IPBC5) is a genotype classified as highly susceptible, with symptom scores ranging from 2 to 4.

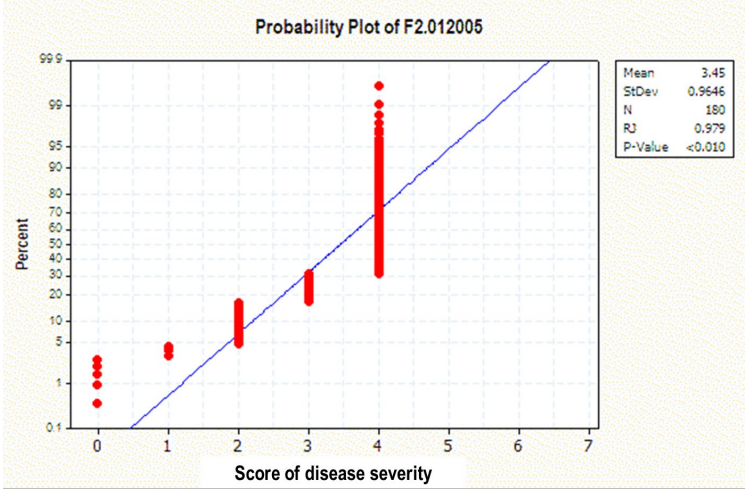

Figure 2. Normal distribution curve of the normality test results of the character score/type of disease symptoms in the F_2 population of IPBC12 × IPBC5 crosses.

Hybrid genotypes resulting from the IPBC12 x IPBC5 cross showed a trend in the distribution of resistance scores closer to the susceptible parent (IPBC5). The susceptible F_1 genotype indicates that chilli resistance to PYLCD is recessive (Basak et al., 2005). The same thing was reported in several studies related to plant resistance to Begomovirus, where the related gene is recessive (Koeda et al., 2021). Traits controlled by recessive genes will only be expressed if their alleles are homozygous recessive. In hybrid conditions (heterozygous), the expression of resistance traits will be covered, which will cause the plant to become susceptible.

The distribution of disease severity in the four populations is visualized in Figure 3. It can be observed that both the F1.012005 and F2.012005 populations exhibit a distribution that more closely resembles that of the susceptible parent. Understanding the pattern of disease severity distribution is essential to infer the type of gene interaction involved.

Table 3. Number of chilli plants in each population of IPBC12 x IPBC5 cross based on yellow curly leaf disease symptom score/type.

Score	Criteria	Number of plants			
		IPBC12	IPBC5	F1.012005	F2.012005
0	Highly Resistant	8	0	0	5
1	Resistant	9	0	0	3
2	Moderate	3	4	2	22
3	Susceptible	0	10	3	26
4	Highly Susceptible	0	6	12	124
Mean		0.75	3.10	3.59	3.45
σ^2		0.72	0.72	0.71	0.96
σ		0.51	0.52	0.51	0.93
CV (%)		95.51	23.17	19.85	27.96

Note: *σ^2 = variance; σ = standard deviation; CV = coefficient of variation.

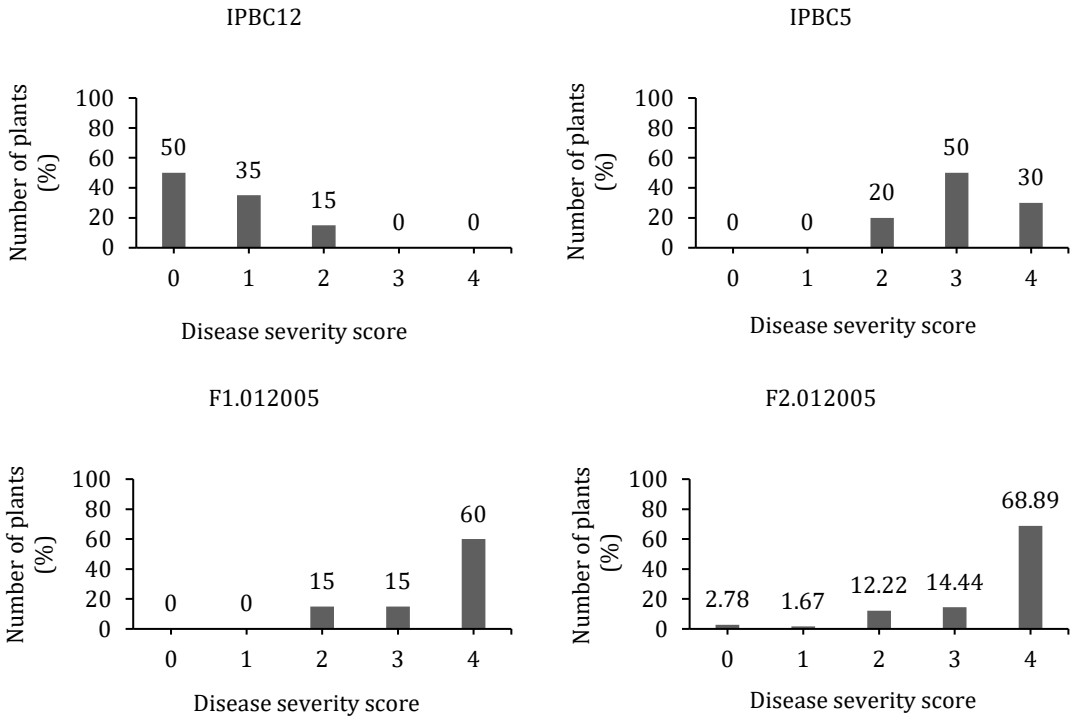

Figure 3. Distribution of pepper yellow leaf curl disease (PYLCD) severity scores in the tested population.

The observed disease symptom scores, representing plant resistance to PYLCD, were used to classify individuals into resistance categories. Three categorizations were applied: two groups, three groups, and four groups of resistance levels. The classifications were tested using Chi-Square analysis, and a summary of the observations and analyses is presented in Table 4.

Tests conducted with two groups of resistance categories (Susceptible and Resistant) showed that the grouping of plant resistance categories was suitable as 13:3 (13 susceptible: 3 resistant). The assumed ratios of 3:1, 15:1, and 9:7 were unsuitable, as indicated by high χ^2 values followed by very low P values. The calculated χ^2 value is higher than the χ^2 table indicates a significant difference between the expected and observed ratios, so the observed resistance level ratio is inconsistent with the expected ratio tested.

Testing the distribution pattern of the resistance level of the F_2 chilli population was also carried out using the expected ratio for three resistance groups: susceptible, moderate, and resistant. A total of four expected ratios were tested in the analysis, namely the ratios of 1:2:1, 9:3:4, 7:6:3, and 12:3:1. Based on the results of the analysis, it was found that the four ratios tested did not match the distribution pattern observed in the F_2 population. The distribution pattern of disease severity in the F_2 population was also tested using four resistance categories: resistant, moderately resistant, moderately susceptible, and susceptible. The results showed that the alternative distribution ratios of 9:3:3:1 and 27:9:9:19 did not match the observed distribution.

Based on the test results in all resistance categories with 15 expected ratios, it can be concluded that the distribution of chilli resistance to Pepper yellow leaf curl disease tends to match the 13:3 ratio. This is the ratio when at least two genes control a character. Both genes have dominant and recessive epistasis interactions.

Table 4. The results of testing the distribution pattern of Pepper yellow leaf curl disease (PYLCD) scores/symptoms in the F_2 population of chilli from the IPBC12 x IPBC5 cross with several possible ratios.

Number of plants	Category*				Expected ratio	df	χ^2 value	P value
	S	MS	MR	R				
180 plants	150	-	-	30	3:1	1	6.67**	0.01
					15:1	1	33.33**	0.00
					9:7	1	53.65**	0.00
					13:3	1	0.51tn	0.47
					37:27	1	48.07**	0.00
					45:19	1	24.62**	0.00
					55:9	1	1.01tn	0.32
180 plants	150	-	22	8	1:2:1	2	326.80**	0.00
					9:3:4	2	57.99**	0.00
					7:6:3	2	114.78**	0.00
					12:3:1	2	6.70*	0.04
					9:6:1	2	55.08**	0.00
					10:3:3	2	36.23**	0.00
180 plants	124	26	22	8	9:3:3:1	3	11.92**	0.01
					27:9:9:19	3	69.51**	0.00

Note: *S = susceptible; MS = moderate susceptible; MR = moderate resistant, R = resistant; df = degrees of freedom; χ^2 = chi-square value; P = significance value of Chi-square test results.

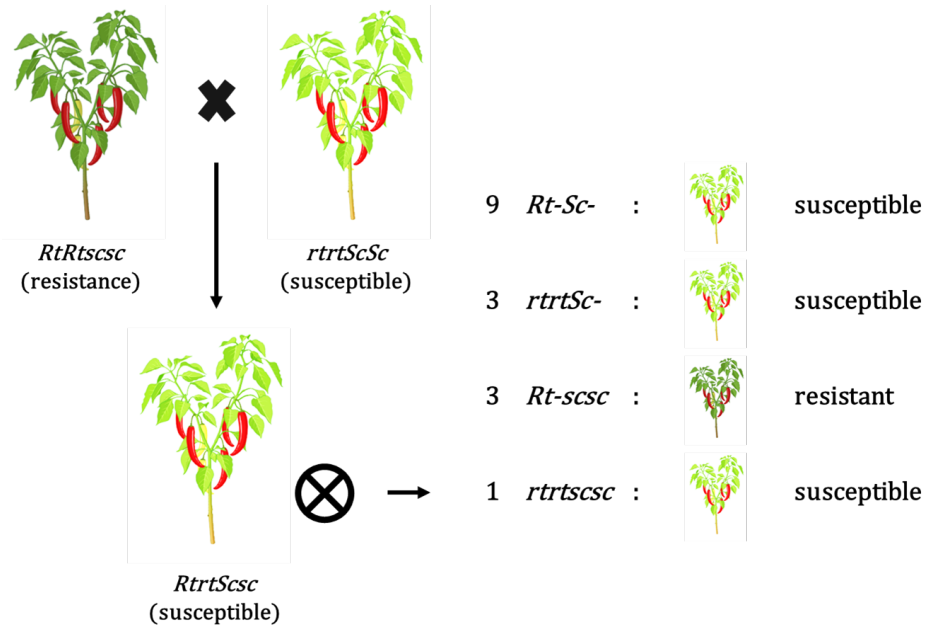

Figure 4. Predicted genetic model for the inheritance of resistance to yellow leaf curl disease in chili pepper.

This 13:3 genotype ratio occurs when there are two interacting genes, where one gene will inhibit the expression of the other gene when it is in the dominant state. As an illustration, a dominant inhibitory gene (*Sc*) will inhibit the expression of a resistance gene (*Rt*). The expression of the Rt (resistance) gene will only be seen when it is dominant, and the inhibitory gene (*Sc*) is homozygous recessive (*RtRtscsc* or *Rtrtscsc*) (Figure 4). Plants become susceptible when the inhibitory gene is dominant (*ScSc*) and when both genes are homozygous recessive (*rtrtscsc*).

Several studies have reported different mechanisms of plant resistance to PYLCD. According to Basak et al. (2005), the distribution of black gram bean resistance to Begomovirus is controlled by a monogenic gene that is fully recessive. Different results were observed in tomato and chilli plants, where the resistance level to PYLCD is thought to involve the role of many genes (Koeda et al., 2020, 2021, 2022). These results align with

the analysis conducted in this study, where the resistance of chilli plants to PYLCD is thought to be controlled by at least two interacting loci.

Research conducted on the model plants *Arabidopsis thaliana*, tomato, and chilli plants indicates that resistance genes can be associated with plant physiological processes. Some genes that have been reported to be related to plant resistance to viruses are genes related to carbohydrate accumulation (Eybishtz et al., 2010), water balance (Sade et al., 2014), and even associated with the repair (Andarwening et al., 2022; Koeda et al., 2021, 2022). When these genes are well expressed, the plant is in an optimum condition, but this optimum condition can be favourable for pathogens. Therefore, plant resistance to pathogens will be formed when these genes are recessive.

Previous research by Ganefianti et al. (2015) showed that a single dominant gene controls PYLCD. However, other research by Koeda et al. (2021) and Koeda et al. (2022) identified two genes suspected of being associated with plant resistance to PYLCD. One gene is dominant (*Pepy-2*) and the other is recessive (*pepy-1*). This result aligns with this study, which suggests that plant resistance is controlled by two genes, each acting as a resistance gene (Rt) and a resistance inhibitor (Sc). Plants are resistant when one resistance gene is dominant and the other (inhibitor) is recessive, and are susceptible when the inhibitor gene is dominant. This interaction leads to plant resistance generally being observed as a recessive trait.

Building on this understanding, future research should focus on elucidating the complex genetic interactions underlying resistance to PYLCD in chili plants, particularly the roles of interacting loci. Investigating the molecular mechanisms by which resistance genes influence plant physiological processes is paramount. Understanding how optimal physiological conditions interact with susceptibility to pathogens may reveal novel strategies to enhance durable resistance through manipulating gene expression or the combination of recessive alleles. This comprehensive approach could support the development of more effective breeding programs targeting multigenic resistance rather than relying on single-gene models.

CONCLUSIONS

The symptom score/type, representing the level of plant resistance to curly leaf disease, was controlled by more than one recessive gene. The distribution of types/scores in the F_2 population followed a ratio of 13:3, with dominance in the susceptible trait. The assumption for this phenomenon is that resistance to PYLCD is controlled by at least two genes that control a character. Both genes have dominant and recessive epistatic interactions.

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