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Spatial Analysis of Viral Outbreaks in Indonesian Tomato Cultivation: Pathways to Sustainable Farming

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Abstract

Tomato production in Indonesia is severely threatened by viral pathogens, compromising yield and food security. This study analyzed the spatial distribution of viral infections in 483 tomato samples collected from 11 provinces spanning 38 districts. Using RT-PCR and PCR diagnostics, we detected an overall infection rate of 96%, encompassing both RNA and DNA viruses. Pepper yellow leaf curl Indonesia virus (PepYLCIV) was the predominant DNA virus, while cucumber mosaic virus (CMV), tobacco mosaic virus (TMV), and tomato mosaic virus (ToMV) were the most widespread RNA viruses, frequently co-infecting with DNA viruses. Mixed infections were common, with up to five viruses detected in single samples, reflecting high viral complexity and crop vulnerability. An inverse relationship between infection complexity and crop vulnerability. An inverse relationship between infection complexity and incidence rate was observed: samples containing more viruses occurred less frequently. The variability of symptoms between single and mixed infections further hinders accurate visual diagnosis, underscoring the need for molecular detection tools. Spatial analysis revealed that Java Island had the highest incidence of viruses and the greatest diversity of combinations. Notably, North Sumatera (Tanah Karo), East Kalimantan (Samarinda and Balikpapan), and Central Sulawesi (Palu, Donggala, and Sigi) also exhibited high virus incidence and frequent DNA–RNA virus coinfections.

Keywords: Indonesia, mix infection, tomato, virus pathogen

Introduction

Tomato (*Solanum lycopersicum* L.) is a major horticultural commodity in Indonesia, playing a critical role in national food security, rural livelihoods, and the agricultural economy. In 2024, national production reached approximately 1.2 million metric tons, with an average annual growth rate of 4.6% over the past five years, reflecting the crop's increasing significance within the country's horticultural sector. Key production areas include West Java, North Sumatra, and West Sumatra, with West Java consistently yielding the highest output. At the regional level, Indonesia ranks as the third-largest tomato producer in the Asia–Pacific region, following China and India, thereby underscoring its strategic position in regional horticulture. According to the Statistik Hortikultura (2024) published by Badan Pusat Statistik, tomato is recognized as one of 18 national priority horticultural commodities. Given the projected annual increase in domestic demand exceeding 5% and the sector's economic importance in agribusiness and rural employment, strengthening tomato production systems is essential to supporting sustainable horticultural development in Indonesia. However, these production systems are often constrained by various factors that reduce yield, particularly biotic stresses. A long-standing challenge in Indonesian tomato cultivation is the prevalence of viral diseases, especially those caused by Begomoviruses. The first documented

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occurrence of tomato-infecting Begomoviruses in Indonesia dates to 1983, with detections in Java and Sumatra linked to substantial yield losses (Kenyon et al., 2014).

Current evidence from regional surveys remains fragmented and geographically constrained, with most studies concentrated on Java Island. The results have revealed substantial Begomovirus diversity in tomato, including ageratum yellow vein virus (AYVV), ageratum yellow vein China virus (AYVCNV), AYVV (Taiwan strain), tomato leaf curl Java virus (ToLCJaV), and pepper yellow leaf curl Indonesia virus (PepYLCIV) in key production regions such as Bandung, Purwokerto, Magelang, and Malang (Sukamto et al., 2005). Subsequent studies expanded this spectrum, identifying tomato yellow leaf curl Kanchanaburi virus (TYLCKaV), PepYLCIV, and tomato leaf curl New Delhi virus (ToLCNDV) across altitudinal gradients in East Java (Lukman et al., 2019), while recent evidence indicates that PepYLCIV has emerged as the dominant Begomovirus in Java (Hermanto et al., 2024). Critically, no nationwide, systematic assessment has quantified the spatial distribution, prevalence, and co-occurrence patterns of Begomoviruses across Indonesia's diverse agroecological zones, including Sulawesi and Kalimantan. This represents a major gap in understanding disease epidemiology in a country with multiple production systems and climatic gradients, limiting the ability to design broadly effective resistance-breeding strategies and region-specific disease management interventions.

Concurrently, the expanding role of RNA viruses is intensifying the epidemiological complexity of tomato viral diseases. The recent detection of tomato mottle mosaic virus (ToMMV) adds to the growing list of RNA pathogens, including cucumber mosaic virus (CMV), tomato mosaic virus (ToMV), tomato chlorosis virus (ToCV), and tomato infectious chlorosis virus (TICV). These viruses are efficiently transmitted via mechanical contact, contaminated seed, and insect vectors such as aphids, facilitating rapid and widespread dissemination. Infection is associated with a broad spectrum of symptoms—including leaf curling, mosaic, chlorosis, stunting, and fruit malformation—that collectively drive significant yield and quality losses.

Materials and Methods

Field Survey and Sample Collection in Tomato Cultivation Areas

Sampling took place in the main tomato cultivation regions of farmers' fields across 11 provinces during the dry season, from July to October 2023. Diseased tomato samples (leaves and fruits) were collected from plants exhibiting symptoms of viral infections, including mosaic, mottling, yellowing, chlorosis, and necrosis, as well as abnormal fruits and leaf deformities such as shoestring, curling, cupping, and stunting. The collected samples were wrapped in paper tissues, placed in paper envelopes, and labeled by collection site. To prevent moisture and decay during transport, the samples were stored in plastic boxes and subsequently kept at -80 °C in the laboratory for subsequent DNA and RNA extraction.

RNA Extraction

Total RNA was extracted using the Plant Virus RNA Kit (Geneaid, Cat. No. PVR050). This kit employs a spin column-based method for the purification of viral RNA from infected plant tissues. Approximately 0.1 mg of fresh tomato leaf tissue was homogenized in a sterile plastic bag with the addition of 1 ml PVR buffer, 100 µl PVRS buffer, and 10 µl β-mercaptoethanol. The homogenate was transferred to a 1.5 ml microcentrifuge tube and incubated at 70 °C for 10 min. Following incubation, the sample was centrifuged at 14,000 rpm for 5 min at 4 °C. A 450 µl volume of the resulting supernatant was transferred to a new tube and mixed with 225 µl of absolute ethanol. The mixture was then loaded onto a PV column and centrifuged at 14,000 rpm for 1 min at 4 °C. The flow-through was discarded, and the column was sequentially washed with 400 µl W1 buffer and 600 µl wash buffer, each followed by centrifugation at 14,000

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rpm for 1 min at 4 °C. A final centrifugation step at 14,000 rpm for 2 min at 4 °C was performed to dry the column matrix. The PV column was then placed into a clean 1.5 ml tube, and 50 µl of RNase-free water was added directly to the center of the column matrix. After a 2-min incubation to allow complete absorption, the column was centrifuged at 14,000 rpm for 1 min at 4 °C to elute the purified RNA.

DNA Extraction

The modified CTAB method was used to extract DNA from infected plants (Aboul-Maaty & Oraby, 2019). The modification made to the protocol was the addition of 50 µl of 10% SDS after the homogenized sample was heated at 65 °C for 15 min and then centrifuged at 4 °C at 17709 RCF for 10 min. 500 µl of supernatant is transferred to a new sterile microtube, then 500 µl of chloroform is added to the supernatant, vortexed, and centrifuged at 4 °C, 14,000 rpm for 10 min. This step was taken 2 times to improve DNA quality. The following steps are the original protocol.

Reverse Transcriptase-Polymerase Chain Reaction (RT-PCR)

RT-PCR was performed using MyTaq One-Step RT-PCR (Bioline, Cat. No. BIO-65049) and the specific primer list in Table 1. Final reaction volume of 10 µl consisted of 5 µl of 2× MyTaq One-Step Mix, 0.1 µl of reverse transcriptase, 0.2 µl of Ribosafe RNase inhibitor, 1 µl of total RNA template, 0.4 µl each of forward and reverse primers, and 2.9 µl of molecular-grade water. Amplification was carried out using a thermal cycler (BioRad T100) under the following cycling conditions: reverse transcription at 45 °C for 20 min, initial denaturation at 95 °C for 1 min, followed by 40 cycles of denaturation at 95 °C for 10 s, annealing for 10 s (temperature dependent on primer specificity), and extension at 72 °C for 30 s. The PCR product is sent for Sanger Sequencing Analysis at FirstBase Malaysia.

Polymerase Chain Reaction (PCR)

PCR was conducted using MyTaq HS Red Mix PCR (Bioline, Cat. No. BIO-25048) and the specific primer list in Table 2. Final reaction volume of 10 µl consisted of 5 µl of 2×

Table 1

Specific Primers Used in RT-PCR Assays for RNA Virus Detection

No	Virus	Group	Amplicon (bp)	TA (°C)	References
1	TICV	*Crinivirus*	432	58.5	PT. East West Seed Indonesia
2	ToCV	*Crinivirus*	366	58.5	PT. East West Seed Indonesia
3	CMV	*Cucumovirus*	386	54.0	(Swapna Geetanjali et al., 2011)
4	ToMV	*Tobamovirus*	362	56.0	(YAN et al., 2021)
5	TMV	*Tobamovirus*	366	60.0	(Sui et al., 2017)
6	ToMMV	*Tobamovirus*	496	48.0	PT. East West Seed Indonesia

Table 2

Specific Primers Used in PCR Assays for DNA Virus Detection

No	Virus	Group	Amplicon (bp)	TA (°C)	References
1	PepYLCIV	*Begomovirus*	432	58.5	PT. East West Seed Indonesia
2	TYLCKaV	*Begomovirus*	366	58.5	PT. East West Seed Indonesia
3	ToLCNDV	*Begomovirus*	386	54.0	PT. East West Seed Indonesia

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Table 3

Virus Identified in the Samples Using Molecular Detection Tools Based on Sampling Regions

No	Province	District	Subdistricts	Village	Elevation (M asl)	Σ samples	Virus detected
1	North Sumatera	Tanah Karo	Berastagi	Sempa Jaya	1397	14	PepYLCIV
			Tiga Panah	Aji jahe	1283	8	PepYLCIV, CMV, TMV, ToMV
			Tiganderket	Tiganderket	922	13	PepYLCV, TYLCKaV, CMV, TMV, ToMV
2	West Sumatera	Agam	Kamang Magek	Kamang Mudiak	1002	11	PepYLCIV, TMV
			Baso	Tabek Panjang	855	4	PepYLCIV
		Tanah Datar	Sungai Tarab	Kumango	753	8	PepYLCIV,TMV, ToCV
			Sepuluh Koto	Koto Baru	1160	11	PepYLCIV, TMV ToMV
		Solok	Sepuluh Koto Diatas	Kuncir	832	6	PepYLCIV
			Gunung Talang	Talang	613	6	PepYLCIVToCV
				Kota Gadang Guguk	974	7	PepYLCIV
		Lima Puluh Kota	Payakumbuh	Sungai beringin	522	5	PepYLCIV
				Piobang	519	4	PepYLCIV
			Harau	Taram	700	4	PepYLCIV, ToCV
3	West Java	Garut	Tarogong Kaler	Pananjung	891	8	PepYLCIV, TYLCKaV, ToLCNDV, TMV
			Banyuresmi	Pamekarsari	723	2	PepYLCIV, ToLCNDV
			Pasirwangi	Sirnajaya	1062	1	PepYLCIV
		Sukabumi	Sukaraja	Langensari	1195	6	CMV
				Selaawi	815	3	CMV
			Sukalarang	Cimangkok	885	3	ToMV
		Cianjur	Gekbrong	Gekbrong	904	3	PepYLCIV, CMV
				Kebon Peuteuy	897	12	PepYLCIV, CMV
			Pacet	Cipendawa	1239	2	PepYLCIV, CMV
		Kuningan	Darma	Gunung Sirah	1393	8	PepYLCIV, CMV, ToCV
		Indramayu	Sliyeg	Sleman	7	8	PepYLCIV, TYLCKaV,
		Lembang	Lembang	Wangunharja	1203	28	PepYLCIV, TYLCKaV, CMV, ToMV, ToCV
		Pangalengan	Pangalengan	Marga Mekar	1430	11	TYLCKaV, CMV, ToMV
				Pulosari	1399	2	CMV
4	Central Java	Purworejo	Ngombol	Wonosari	8	8	PepYLCIV, CMV, TMV
			Purwodadi	Geparang	9	7	PepYLCIV, CMV, TMV
		Magelang	Pakis	Kaponan	1149	7	PepYLCIV, CMV
			Sawangan	Pathuk mangunsari	421	6	PepYLCIV, TYLCKaV, CMV
		Wonosobo	Kalijajar	Wonokrio	1097	11	PepYLCIV, CMV, ToMMV

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Table 3 (continued)

Virus Identified in the Samples Using Molecular Detection Tools Based on Sampling Regions

No	Province	District	Subdistricts	Village	Elevation (M asl)	Σ samples	Virus detected
5	East java	Lumajang	Candipuro	Sumber Mujur	805	25	PepYLCIV, CMV, TMV, ToMV
		Malang	Wajak	Patok Picis	597	7	PepYLCIV, TYLCKaV, CMV, TMC, ToMV
			Poncokusumo	Karang Anyar	603	6	PepYLCIV, TYLCKaV, CMV, TMV, ToMV
			Pujon	Pujon Kidul	1101	11	PepYLCIV, CMV, TMV, ToMV
		Banyuwangi	Licin	kluncing	1120	4	PepYLCIV, CMV, TMV, ToMV
		Bondowoso	Jambesari	Grujuganlor	288	2	PepYLCIV, TYLCKaV, CMV, TMV, ToMV
			Pujer	Kejayan	309	8	PepYLCIV, TYLCKaV, ToLCNDV, CMV, TMV, ToMV
		Blitar	Wonodadi	Kebon Agung	105	4	PepYLCIV, TYLCKaV, CMV, TMV, ToMV
			Srengat	Dermojayan	122	7	PepYLCIV, TYLCKaV, CMV, TMV, ToMV
6	Bali	Bangli	Kintamani	Yahmampa	1404	15	PepYLCIV, CMV, TMV, ToCV
				Songan	1132	3	PepYLCIV
		Klungkung	Banjarangkan	Bungbungan	378	4	pepYLCIV
7	West Nusa tenggara	Lombok Tengah	Batukliang	Tanak Beak	298	6	PepYLCIV, TMV, ToCV
				Tratak	378	8	PepYLCIV, TMV, ToCV
		Lombok Timur	Sembalun	Sembalun Bumbung	1445	7	PepYLCIV, ToMV
				Sembalun Lawang	1216	4	PepYLCIV, ToCV, TICV
8	East Kalimantan	Penajam	Penajam	Nipah-Nipah	17	3	PepYLCIV
				Api- Api	56	1	none
				Girimukti	20	5	TYLCKaV, TMV, ToCV
			Babulu	Babulu Barat	12	6	PepYLCIV, TYLCKaV, TMV
		Kutai Kartanegara	Muara Badak	Batu-Batu	70	21	PepYLCIV, TYLCKaV, TMV, ToCV
		Samarinda	Samarinda Utara	Lempake	6	14	PepYLCIV, TYLCKaV, ToLCNDV, CMV, TMV, ToCV
			Balikpapan Timur	Manggar	8	4	PepYLCIV, TYLCKaV, ToLCNDV, CMV, TMV

Table 3 (continued)

Virus Identified in the Samples Using Molecular Detection Tools Based on Sampling Regions

No	Province	District	Subdistricts	Village	Elevation (M asl)	Σ samples	Virus detected
9	South Sulawesi	Enrekang	Baroko	Benteng Alla	1093	18	PepYLCIV, CMV, ToCV
			Masale	Rampunan	1111	6	PepYLCIV, CMV, TMV, ToCV
				Masale	1120	4	PepYLCIV, ToCV
		Pinrang	Patampanua	Padangloang	46	3	PepYLCIV, CMV, TMV
10	Central Sulawesi	Palu	Tatange	Boyoage	21	10	PepYLCIV, ToLCNDV, CMV, ToMV, ToCV
		Donggala	Labuan	Labuan Lelea	28	6	PepYLCIV, CMV, TMV, ToCV
		Sigi	Kinovaro	Porame	205	6	PepYLCIV, ToLCNDV, CMV, TMV, ToMV, ToCV
			Marawola	Binangga	34	1	PepYLCIV, CMV, TMV, ToMV
			Dolo	Karawana	65	4	PepYLCIV, CMV, TMV, ToMV, ToCV
			Sigibiromaru	Kalukubula	27	4	PepYLCIV, CMV, TMV, ToMV, ToCV
11	North Sulawesi	Bolaang Mongondow Timur	Modayag Barat	Mongkudai	684	1	CMV
			Modayag Barat	Sumberejo	1100	1	CMV
		Minahasa Selatan	Modoinding	Sinisir	620	1	CMV
		Minahasa Utara	Kauditan	Kauditan	208	1	CMV
		Minahasa	Langowan Barat	Tuamaratas	844	1	CMV
			Tampaso	Tampaso	743	1	CMV
		Tomohon	Tomohon Timur	Rurukan	917	1	CMV
		Bone Bolango	Tilongkabila	Moutong	31	2	PepYLCIV, ToLCNDV, CMV

MyTaq HS Red Mix, 1 µl of total DNA extract, 0.5 µl each of forward and reverse primers, and 3 µl of molecular-grade water. Amplification was performed using a thermal cycler (BioRad T100) under the following conditions: initial denaturation at 95 °C for 3 min, followed by 40 cycles of denaturation at 95 °C for 15 s, primer-specific annealing for 15 s, and extension at 72 °C for 30 s, with a final elongation step at 72 °C for 3 min. PCR products were analyzed by electrophoresis on a 1.5% agarose gel stained with GelRed (Biotium) to verify the presence of DNA fragments of the expected size. The PCR product was continued for Sanger Sequencing Analysis in FirstBase Malaysia.

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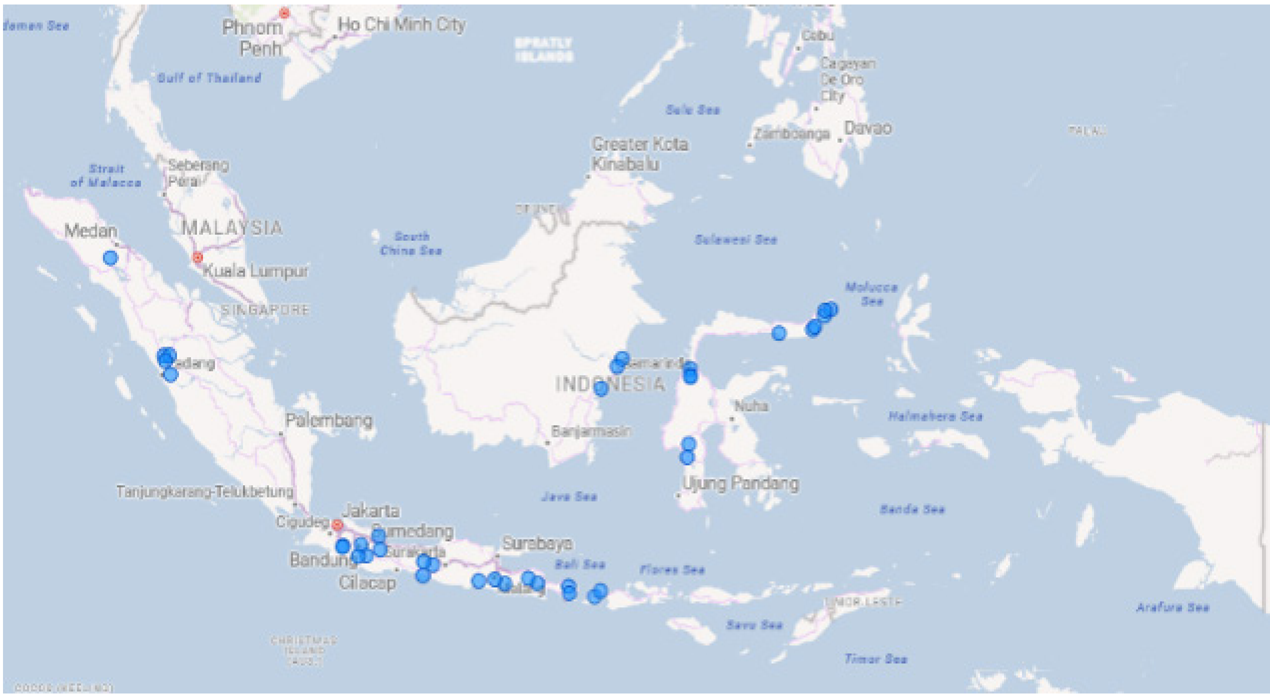
Figure 1

Distribution Map of Tomato Sampling Areas Based



Results and Discussions

Survey and Sampling Coverage of Tomato Cultivation Areas

A total of 483 leaf samples of tomato plants exhibiting virus symptoms were collected from 38 districts across 11 provinces in Indonesia during the dry season of July–October 2023 (Figure 1). Sampling coverage reflected the country's major tomato-producing regions, with Java Island contributing the largest share of samples. West Java accounted for 97 samples from Cianjur, Sukabumi, Garut, Kuningan, Indramayu, Lembang, and Pangalengan; Central Java contributed 39 samples from Purworejo, Magelang, and Wonosobo; and East Java contributed 74 samples from Lumajang, Malang, Blitar, Bondowoso, and Banyuwangi. Outside Java, 35 samples were collected from Tanah Karo in North Sumatra, and 66 samples were obtained from Agam, Tanah Datar, Solok, and Limapuluh Kota in West Sumatra. Additional sampling included 22 samples from Bangli and Klungkung in Bali, 25 from Central and East Lombok in West Nusa Tenggara, and 54 from Penajam, Kutai Kartanegara, and Samarinda in East Kalimantan. Sulawesi was represented by North, Central, and South Sulawesi, encompassing 11 districts, with Central and South Sulawesi contributing 71 samples in total. Overall, the sampling distribution highlights the concentration of tomato cultivation in Java and other major production centers across Indonesia.

Molecular Diagnosis of Viruses in Collected Samples

All leaf samples were tested using RT-PCR for RNA viruses (Table 1) and PCR for DNA viruses (Table 2). Of 483 samples, 464 tested positive for at least one virus (96% infection rate); 19 symptomatic samples were negative for all targeted viruses, suggesting the presence of undetected or uncharacterized agents. Among positive samples, 76 contained only RNA viruses, with CMV most frequently detected, followed by TMV, ToMV, ToCV, and TICV (lowest). Mixed

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RNA infections were common, especially CMV–ToMV, while triple infections were rare (Figure 2). Among DNA viruses, 145 samples were solely infected with Begomovirus, with PepYLCIV dominating (~125 cases). Only 7 samples contained TYLCKaV alone, while 13 had mixed Begomoviral infections (PepYLCIV, TYLCKaV, ToLCNDV), highlighting complex interactions. Table 3 systematically presents sample origins, elevation ranges, and viral detection results to support interpretation. Molecular diagnostics also revealed high mix-infection complexity, with up to five viruses (both RNA and DNA) detected in single plants. An inverse relationship between infection complexity and incidence rate was observed: samples with more viruses were less frequent (Figure 4), suggesting that viral interactions influence infection dynamics.

Spatial Distribution of Tomato Viral Pathogens Across Surveyed Regions

The geographic distribution of RNA viruses across Indonesia is shown in Figure 5. CMV was the most widespread, detected in West Java, Central Java, East Java, Bali, and

Figure 2

Prevalence and Distribution of RNA Virus Infections and Their Mixed-Infection Profile

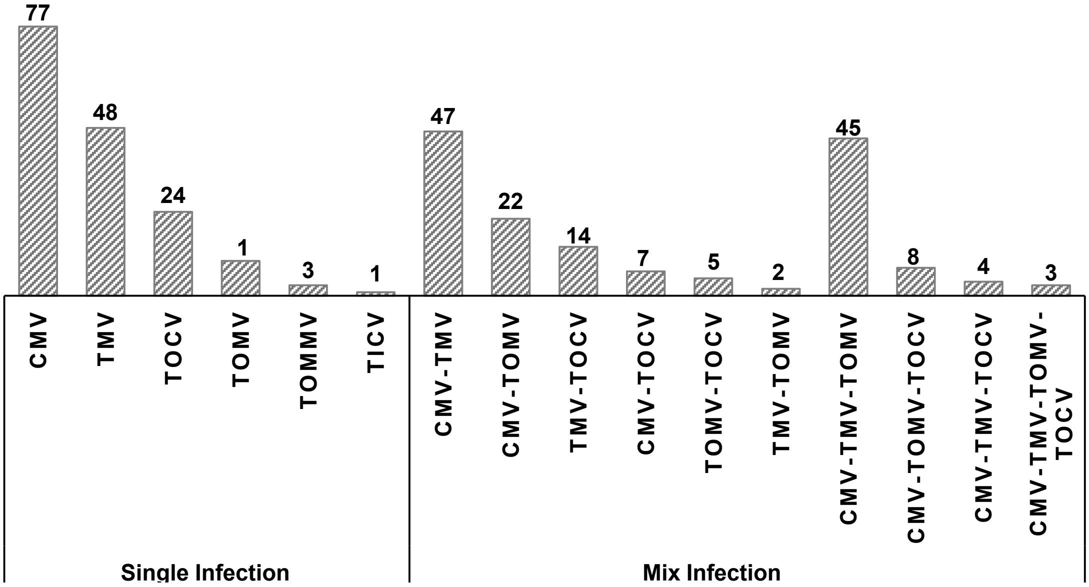

Figure 3

Prevalence and Distribution of DNA Viruses' Infection and Their Mixed-Infection Profile

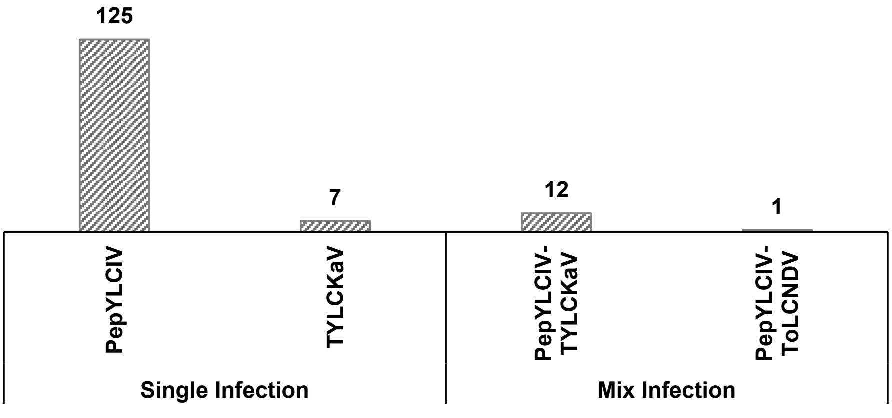

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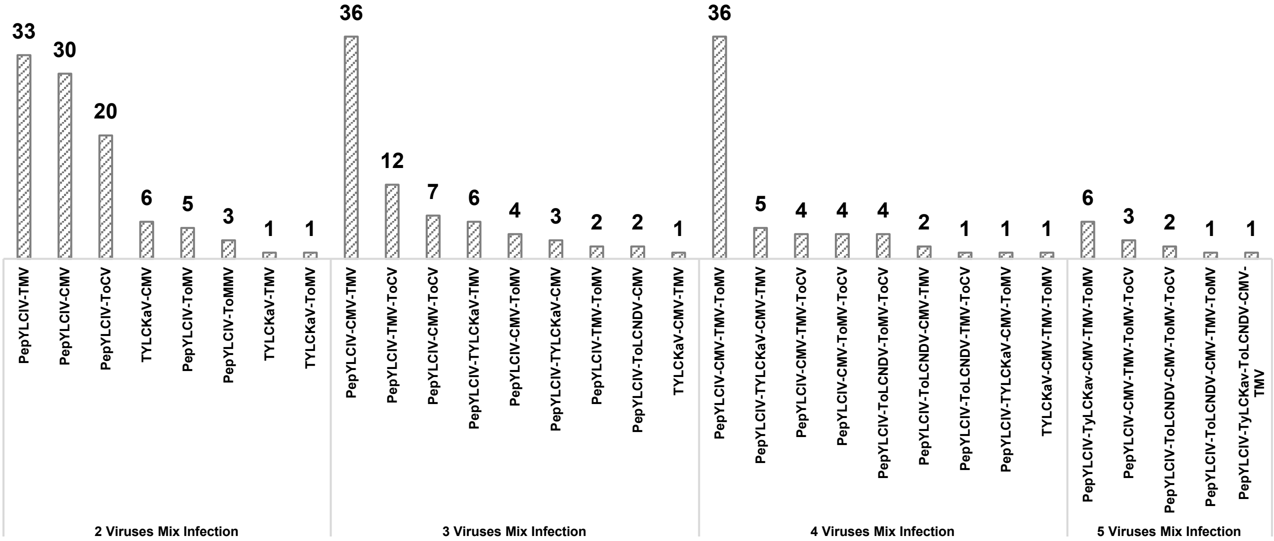
Figure 4

Prevalence and Distribution of DNA-RNA Viruses Mix Infection Profile



South Sulawesi, reflecting its broad host range and aphid-mediated transmission. TMV occurred in West Java and East Kalimantan, likely due to mechanical transmission and environmental stability. ToMV was mainly confined to West Java, suggesting localized cultivation practices or effective sanitation. ToCV was detected in Central Java and Bali, consistent with the presence of whitefly vectors, whereas TICV was interestingly restricted to West Nusa Tenggara, suggesting limited spread or recent emergence. This heterogeneous distribution highlights differing transmission dynamics and the need for ongoing surveillance.

DNA virus distribution (Figure 6) shows PepYLCIV is widespread across major tomato-growing regions, whereas TYLCKaV is largely confined to northern Java (Semarang, Pekalongan, Cirebon). Both cause severe symptoms like stunting, leaf curling, and yield loss. High Begomovirus incidence in these areas likely stems from intensive cultivation and high whitefly populations. In West and Central Java, mixed Begomovirus infections involving ToLCNDV are frequent, indicating strong viral pressure and complex interactions that may worsen disease severity. Overall, Java is a hotspot for both single and mixed DNA virus infections due to intensive agriculture and favorable vector conditions.

Figure 7 illustrates the geographic distribution of mixed DNA–RNA virus infections, which predominantly involve Begomoviruses transmitted by *Bemisia tabaci* in combination with RNA viruses. Highly complex coinfections—defined as the presence of more than two viruses per host—are largely confined to the intensively cultivated regions of Java, underscoring its role as a major hotspot for viral accumulation and transmission. Spatial analysis further revealed that DNA–RNA coinfection combinations were detected not only in Java but also in North Sumatra (Tanah Karo), East Kalimantan (Samarinda and Balikpapan), and Central Sulawesi (Palu, Donggala, and Sigi), highlighting the expanding geographic footprint of these viral pathogens across Indonesia.

Symptom Variation in Single and Mixed Infections Limits Rapid Field Diagnosis of Tomato Viruses

In samples confirmed by PCR to be infected with RNA viruses (Figure 8), a wide range of foliar symptoms was observed, reflecting the diversity of the viral pathogens involved. CMV infections induced mild to severe leaf curling, often accompanied by chlorosis,

Figure 5

Distribution Map of RNA Virus Infecting Tomato Plants in Indonesia

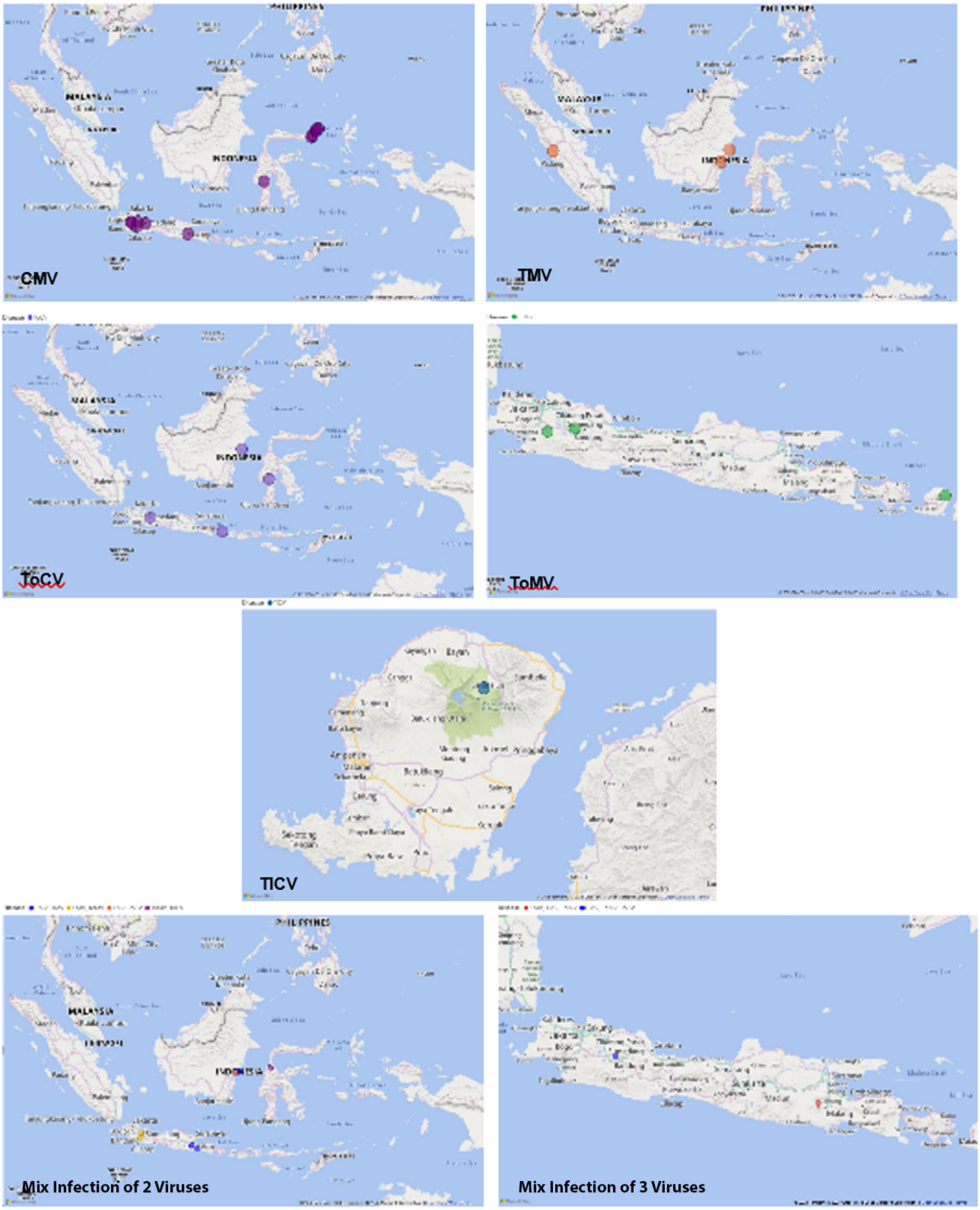


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Figure 6

Distribution Map of the DNA Virus Infecting Tomato in Indonesia

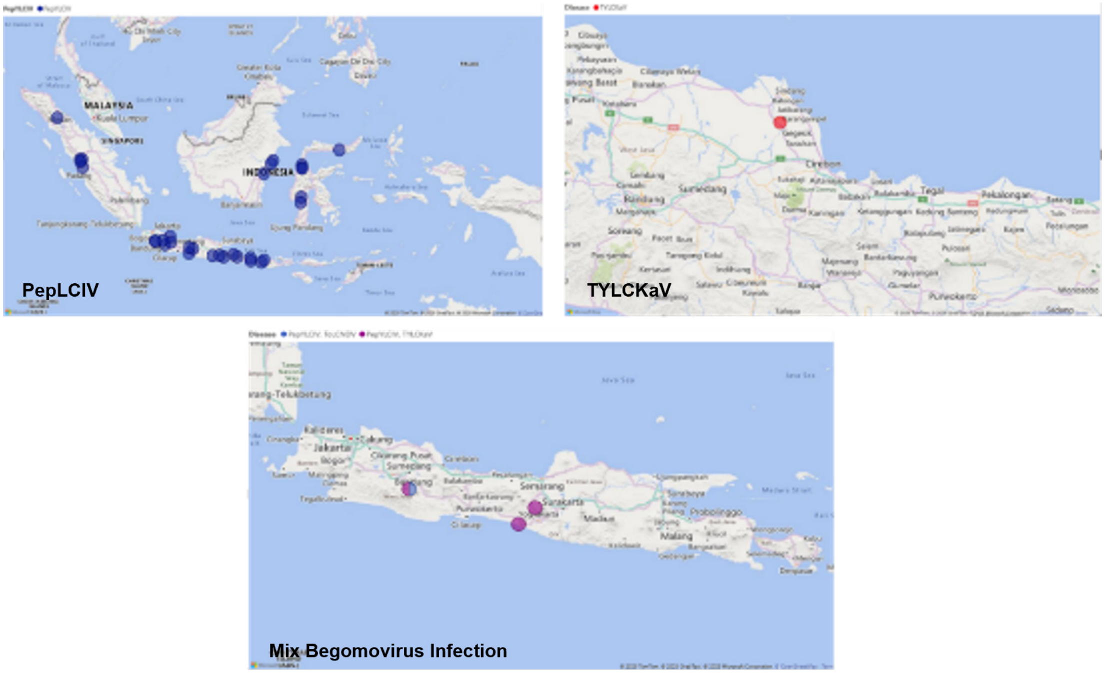
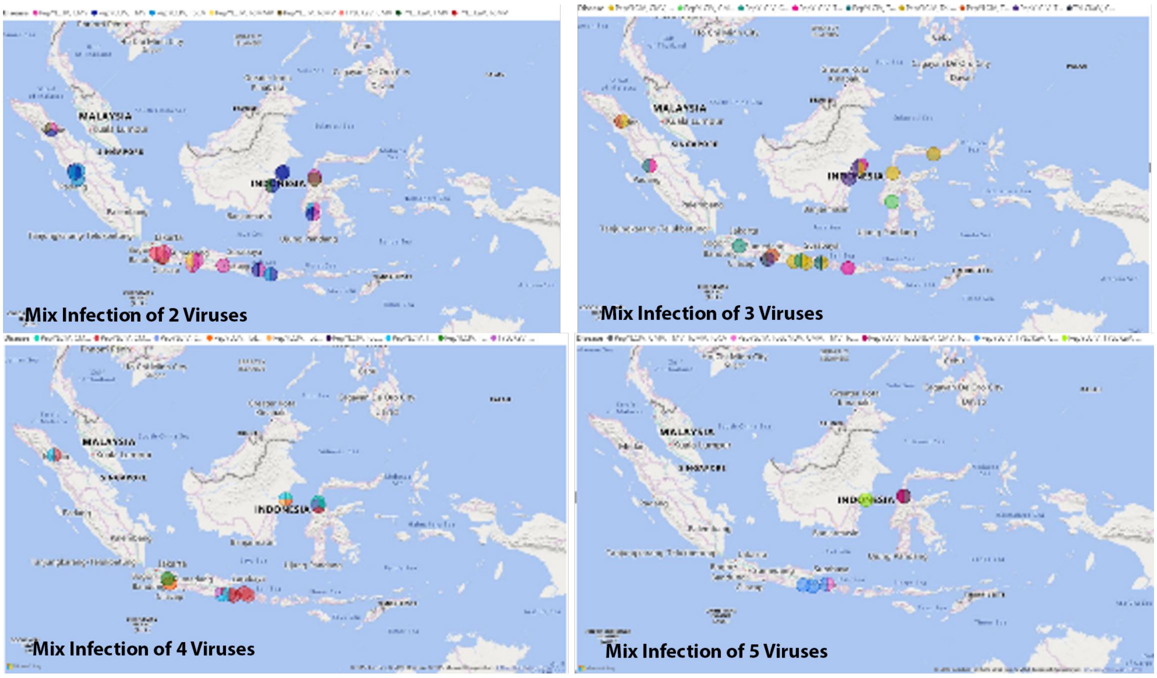


Figure 7

Distribution Map of DNA-RNA Virus Mix Infection Infecting Tomato in Indonesia



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whereas ToCV was associated with mottled yellow patches, marginal necrosis, and mild leaf curling. ToMV caused more severe symptoms, including pronounced mottling and extensive leaf deformation. Symptom severity was markedly enhanced in mixed infections, such as CMV–ToMV and CMV–ToMV–ToCV, which exhibited intensified leaf curling, widespread chlorosis, and necrosis, indicating synergistic virus–virus interactions. Fruit symptoms, including uneven ripening and discoloration, were observed in CMV- and ToMV-infected plants and were more pronounced under mixed infections, often presenting as irregular ripening and fruit deformities.

Similarly, both single and mixed Begomovirus infections (Figure 9) and DNA–RNA virus coinfections (Figure 10) produced considerable variability in symptom expression. These included leaf curling without yellowing, reduced leaf size and deformation without chlorosis, leaf cupping, and curling accompanied by yellowing. Overall, this diversity of symptoms underscores the complexity of virus–host interactions; it demonstrates that a single virus or combination of viruses can induce multiple symptom phenotypes depending on host genotype, environmental conditions, and infection stage. Symptom variability across single and multiple infections further complicates visual diagnosis, underscoring the need for molecular detection tools.

Figure 8

Symptom Variability in Tomato Plants and Fruits Infected by Single and Mixed RNA Viruses

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Figure 9

Symptom Variability in Tomato Plants and Fruits Infected by Single and Mixed DNA Viruses

Figure 10

Symptom Variability in Tomato Plants by Mixed DNA and RNA Viruses

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Discussions

In this study, CMV was identified as the most widely distributed RNA virus, occurring across multiple provinces. Previously reported, CMV induces visible symptoms in 37 host species, and weeds can serve as important virus reservoirs. Symptom expression includes both local lesions, such as chlorotic spots and necrosis, and systemic manifestations, including mosaic and mottling. Symptom onset ranged from 2 to 28 days after inoculation. Plant families such as Amaranthaceae and Cucurbitaceae exhibited both local and systemic symptoms, whereas other families showed only local lesions. In contrast, some species, including *Solanum melongena*, *Zea mays*, and *Arachis hypogaea*, remained asymptomatic. In tomato, CMV infection is associated with severe symptoms, including stunting, yellowing, mottling, and pronounced leaf deformation, such as filiform or “shoestring” leaves (Jalender, 2015). Such symptoms may result in substantial yield losses, emphasizing the importance of early detection and effective disease management. Previous reports have also shown that CMV is not seed-borne in tomato but is transmitted primarily by aphids, with wild plants and weeds serving as important sources of inoculum. Therefore, weed management and vector control are critical components of CMV prevention in tomato cultivation. In addition, experimental evaluations of tomato genotypes have demonstrated considerable variability in response to CMV infection. Highly susceptible genotypes showed disease severities ranging from 88.88% to 100%, indicating extreme vulnerability to the virus. In contrast, partially resistant genotypes exhibited markedly lower disease severities of 2.22%, 6.66%, 8.88%, and 20%, respectively, highlighting the potential value of host resistance in CMV management. (Al-Shammari et al., 2023).

Another RNA virus identified in this study was TMV. This virus has historical significance, as its discovery marked a major milestone in the development of virology following severe tobacco disease outbreaks in Europe during the mid-19th century. Tobamoviruses, including TMV and ToMV, are well recognized as causal agents of mosaic diseases in tomato, resulting in substantial yield losses and deterioration of fruit quality. During the early 20th century, both TMV and ToMV posed serious threats to the tobacco and tomato industries. For many years, these viruses were effectively managed through resistance breeding, particularly by the deployment of the Tm-1 and Tm-2^2 resistance genes. However, the recent emergence of new tobamoviruses, such as tomato mottle mosaic virus (ToMMV) and tomato brown rugose fruit virus (ToBRFV), has challenged this control strategy by overcoming previously effective resistance genes and triggering outbreaks in tomato-growing regions worldwide (Ishibashi et al., 2023). In addition, other reports exhibiting co-infection ToMMV with ToCV or PepYLCIV. This finding represents the first report of ToMMV infecting tomato crops in Indonesia and Southeast Asia (Kwak et al., 2025). These results highlight the importance of implementing integrated disease management, strengthening seed quality control, and developing region-specific management strategies.

Geminiviruses, which are DNA viruses, are classified into nine distinct genera: Begomovirus, Becurtovirus, Capulavirus, Curtovirus, Grablovirus, Eragrovirus, Mastrevirus, Topocuvirus, and Turncurtovirus. Their transmission depends on a range of insect vectors, including whiteflies, aphids, leafhoppers, and treehoppers (Brown et al., 2015; Varsani et al., 2017). Among those genera, Begomoviruses stand out for their global prevalence and their specific infection of dicotyledonous plants. They are primarily spread by whiteflies through a semi-persistent calculative process, meaning the virus travels through the insect’s body without replicating inside it. However, recent discoveries have challenged this understanding. For instance, TYLCCNV has been shown to replicate within the salivary glands of whiteflies, utilizing the insect’s own DNA replication mechanisms. This suggests a more intricate virus-vector relationship than previously thought, with potential implications for how these viruses are transmitted (Czosnek et al., 2017). Interestingly, Begomoviruses are not

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solely dependent on insect vectors. Emerging evidence indicates that some species, such as TYLCTHV, ToLCTV (Chang et al., 2023), and ToLCNDV (Devi et al., 2023; Fortes et al., 2023), can also be transmitted through seeds, adding another layer of complexity to their epidemiology.

PepYLCIV has been identified as a widely distributed DNA virus, with confirmed infections reported in 30 districts across various regions. The virus was first documented in 1999, initially infecting chili pepper crops in West Java (Hidayat et al., 2006). Since its initial discovery, PepYLCIV has demonstrated a remarkable capacity for rapid dissemination, eventually establishing itself as a major pathogen in tomato cultivation. Its spread has been particularly devastating in chili-pepper-growing regions throughout Indonesia, where it has been associated with crop losses of up to 100% (Gede et al., 2021). Subsequent research has expanded the known host range of PepYLCIV beyond chili and tomato. A study conducted in Yogyakarta, Central Java, revealed that the virus can also infect eggplants and *Ludwigia* species, indicating its adaptability to diverse plant hosts (Annisaa et al., 2021). Furthermore, a broader survey of Begomovirus infections in tomato-producing areas across Java Island—including West, Central, and East Java—confirmed that PepYLCIV has become the predominant Begomovirus, surpassing other species such as TYLCKaV and ToLCNDV in prevalence (Hermanto et al., 2024). The extensive distribution and high incidence of PepYLCIV may be attributed not only to its broad host range but also to its multiple transmission pathways. While whiteflies are recognized as the primary vector, recent studies have also confirmed that PepYLCIV can be transmitted through seeds (Fadhila et al., 2020; Sudarsono et al., 2023). This dual mode of transmission—both vector-borne and seed-borne—likely plays a significant role in facilitating the virus's rapid and widespread dissemination, posing a serious threat to the sustainability of solanaceous crop production in Indonesia.

TYLCKaV is believed to have originated in Thailand, where it was initially identified infecting eggplants. Its presence in Indonesia was first documented in 2013, specifically in the provinces of West Java and Central Java, where infected eggplants exhibited pronounced chlorosis symptoms on their foliage (Kintasari et al., 2013). In 2019, a study surveyed the diversity and distribution of Begomovirus infections in Solanaceae crops (tomato, pepper, and eggplant) across three altitudes in East Java, Indonesia—Kencong (low), Karangploso (mid), and Pujon (high). Using a multiplex PCR assay, four Begomovirus species were detected: PepYLCIV, TYLCKaV, ToLCNDV. Tomato was infected by PepYLCIV, TYLCKaV, and ToLCNDV, both as single and mixed infections. Mixed infections were most frequent in Kencong, with combinations such as PepYLCIV–TYLCKaV, PepYLCIV–ToLCNDV, and triple infections involving all three viruses. In Pujon, mixed infections were also observed, while Karangploso had fewer detections. The study found that Solanaceae crops had higher Begomovirus infection rates at high altitudes (96.6%) compared to mid (65%) and low (83.3%) altitudes. However, virus species occurrence was more influenced by crop type than altitude (Lukman et al., 2019). These co-infections may exacerbate disease severity and complicate management strategies. Notably, the Indonesian variant of TYLCKaV has been classified as a bipartite Begomovirus, meaning its genome is divided into two distinct components, a characteristic confirmed through molecular studies (Kikkawa et al., 2023). Another Begomovirus identified in the analyzed tomato samples was ToLCNDV, which was consistently detected in mixed infections rather than as the sole pathogen. The phenomenon of multi-virus infections in tomato crops has long been recognized, involving not only viruses from the same genus but also across different genera. For example, co-infections have been reported between ToLCNDV-ES and TYLCV (Vo et al., 2022). Another study revealed that tomato plants in East Java were infected by three Begomovirus species—ToLCV, TYLCV, and PepYLCV — with ToLCV being the most dominant in low-altitude areas (Kencong). Mixed infections were common, especially in Kencong, leading to severe and varied symptoms, including mosaic, leaf curling,

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cupping, and dwarfing. Phylogenetic analysis showed that ToLCV isolates from tomato in Kencong were closely related to ToLCNDV from cucumber in Central Java, suggesting regional virus movement. Molecular detection confirmed that tomato is highly susceptible to complex Begomovirus infections that vary with altitude and environmental conditions (Sidik et al., 2023). Additionally, the study on pepper found similar result that Begomovirus infection rates in pepper plants were extremely high in Java, with 93% incidence in lowlands and 88.78% in highlands, and disease severity was significantly greater in lowlands (54.5%) compared to highlands (38.1%). The most dominant and severe virus was PepYLCIV, occurring both as a single infection and in combination with TYLCKaV. The primary vector identified was *Bemisia tabaci* biotype B, and mixed infections were more frequent and severe in lowlands (Wahyono et al., 2023).

These findings highlight the dynamic nature of Begomovirus infections, in which multiple viruses can coexist and interact synergistically or antagonistically, influencing disease severity, transmission efficiency, and management outcomes. The wide variation and overlap of symptoms in virus-infected plants result from complex interactions among viral virulence, host genotype, physiological condition, and environmental factors such as light and temperature, with additional influence from infection timing and strain-level genetic variation. Because these factors can produce similar symptoms across different viruses and mixed infections, visual diagnosis alone is unreliable; therefore, accurate identification requires molecular methods, such as PCR, to ensure proper diagnosis and effective disease management (Jiang & Zhou, 2023; Rojas et al., 2018).

Spatial analysis pinpointed Java Island as the predominant hotspot for both single and mixed infections; however, high viral incidence and DNA–RNA coinfection combinations were also documented in North Sumatra (Tanah Karo), East Kalimantan (Samarinda and Balikpapan), and Central Sulawesi (Palu, Donggala, and Sigi), indicating an expanding geographical range of these pathogens. The considerable variation in symptom expression between single and mixed infections further impedes reliable visual diagnosis, underscoring the essential requirement for molecular detection tools to precisely identify viral pathogens and inform management strategies. To gain a more comprehensive understanding of the epidemiological landscape, future surveys should be extended to under-sampled regions, including Sumatra (apart from North Sumatra), Kalimantan (apart from East Kalimantan), Sulawesi (apart from Central Sulawesi), Papua, and the Maluku Islands, where viral diversity and potential emergence remain largely uncharacterized. Furthermore, the systematic collection and characterization of insect vectors—particularly whiteflies (*Bemisia tabaci*), aphids, and thrips—are necessary to confirm transmission routes, track vector population dynamics, and forecast disease outbreaks. Such integrated surveillance, which combines expanded geographic sampling with vector ecology studies, will enhance regional capacity for the early detection and sustainable management of viral diseases affecting tomato production.

Conclusions

This study confirms pervasive viral threats to Indonesian tomato production, with a 96% infection rate and frequent mixed infections involving up to five viruses per plant. PepYLCIV was the predominant DNA virus, while CMV, TMV, and ToMV were the most widespread RNA viruses, often co-infecting with DNA viruses. Spatial analysis identified Java as the primary hotspot, but high virus incidence and DNA–RNA coinfections in North Sumatera, East Kalimantan, and Central Sulawesi indicate an expanding geographic footprint. Variable symptom expressions across infection types complicate visual diagnosis, underscoring the need for molecular detection tools. Future surveys should target underserved regions (Sumatra, Kalimantan, Sulawesi, Papua, Maluku), while systematic vector surveillance—

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focusing on whiteflies, aphids, and thrips—is essential for confirming transmission pathways and predicting outbreaks. Integrated geographic and vector-based surveillance will strengthen early detection and sustainable management of tomato viral diseases.

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