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SILENT SYNERGIES: MIXED INFECTIONS OF VIRUS AND PHYTOPLASMA AND THEIR EPIDEMIOLOGICAL SIGNIFICANCE IN CRUCIFEROUS CROPS

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ABSTRACT

Cruciferous crops are an integral part of global food and nutritional security, but they are increasingly challenged by complex disease scenarios involving multiple pathogens. Among various pathogens attacking the crop, simultaneous occurrence of various plant viruses and virus with phytoplasmas have emerged as significant threat for production of the crops. Traditionally the pathogens were studied in isolation but now these pathogens are recognized to frequently co infect crops, giving rise to intricate disease expressions that are often overlooked. Such mixed infections can enhance disease severity, disrupt normal plant functions and lead to substantial yield and quality loss. This review brings together the current knowledge on the prevalence and epidemiology of virus - virus and virus-phytoplasma mixed infections in cruciferous crops. The challenges associated with symptom-based diagnosis and the need for advanced molecular tools for accurate detection are discussed. The shift in the perspective from single pathogen to a more complex understanding of disease occurrence emphasizes the need to adopt holistic approaches in research and crop protection. Addressing the mixed infections is essential not only for improving the disease management but also ensuring sustainable production of cruciferous crops in changing ecosystems.

Keywords **:** Crucifers, virus, phytoplasma, mixed infection.

Introduction

Crucifers, belonging to family Brassicaceae, consists of a large number of economically important vegetable crops such as mustard, raddish, cabbage, kale, broccoli, cauliflower, etc. in addition to various ornamentals, condiments, besides including more than 130 species of cosmopolitan weeds (Lai *et al.*, 2025). It is considered as a large family which has native species in almost all continents except Antarctica (Al-Shehbaz, 2025). These crops share some similar features such as pungent odour which is due to glucosinolates, presence of siliques, tetradynamous stamens and cruciform corolla. It is reported that the Brassicaceae family consists of 352 genera and the species ranges between 3350 to 3660 (Zhou *et al*., 2024). These plants can grow at various types of habitats, of which some are very extreme. The cruciferous crops contribute immensely to global nutrition and agricultural economies. These crops are always under attack by a wide range of pathogens, especially viruses and phytoplasmas, that significantly affect the quality of produce, thereby reducing the yield.

In recent years, there has been a significant shift in the classical concept of ‘one disease, one pathogen’ in plant disease etiology to a more complex understanding which involves mixed infections (Yu and Wei, 2025). Under this concept, multiple pathogens can co-exist within the same host at the same time. Various evidences suggest that, in cruciferous crops like cabbage, cauliflower, mustard, broccoli, mixed infections by viruses and phytoplasma are becoming increasingly common in field conditions (Bertaccini *et al*. 2014; Kumari *et al*., 2019). Such co-infections often lead to changes in symptom expression, increased severity of disease and altered epidemiology (Xu *et al.*, 2022). Cruciferous crops are highly vulnerable to such mixed-infections especially due to intense cultivation and exposure to environment

where vector population is high (Yu and Wei, 2025). This review focuses mainly on the current knowledge of mixed infection among various types of viruses and also between virus and phytoplasmas in crucifer crops.

Overview of phytoplasmas and viruses infecting crucifers

Phytoplasmas are prokaryotic, phloem limited, wall-less plant pathogens that are transmitted by phloem feeding insect vectors like green leaf hoppers and plant hoppers (Rao *et al.,* 2017). They have a size ranging between 200 to 800 nm, pleomorphic in shape having a wide host range (Bertaccini *et al.* 2014; Rao *et al.,* 2011). The most typical symptoms produced by phytoplasmas are phyllody, witches' broom, virescens and stunting and they are known to infect hundreds of plant species (Bertaccini, 2022; Kumari *et al*., 2019). With advances in molecular detection techniques, some studies have reported wide diversity among them. Phytoplasma belonging to sub groups such as 16SrI, 16SrII, 16SrIII, 16SrVI and 16SrXV-A are frequently reported to infect cruciferous vegetables (Kumari *et al*., 2019). Zhang *et al.,* (2020) reported the infection of 16SrVI-A Phytoplasma in spring oilseed mustard in Mongolia, China. Zwolinska *et al*., (2019) found that a Phytoplasma of the sub group 16SrI-B of 'Candidatus Phytoplasma asteris' cause disease in *Brassica napus.* Cai *et al.,* (2016) identified phytoplasma belonging to sub group 16SrI and 16SrII infecting cabbage and cauliflower, which showed symptoms of proliferation of axillary buds, crinkled leaves and plant stunting with shortened internodes.

Similarly plant viruses also create significant difficulties in the cultivation of crops. In cruciferous systems, *Turnip mosaic virus* (TuMV), *Cauliflower mosaic virus* (CaMV), *Brassica yellows virus* (BrYV) *Cucumber mosaic virus* (CMV), etc. are widely prevalent, that not only reduce the quality of these crops, but also bring down the yield (Sevik, 2016). Out of various viruses attacking crucifers, the *Turnip mosaic virus* and *Cucumber mosaic virus* are more common. *Turnip mosaic virus* is a positive stranded RNA virus which belongs to genus potyvirus (Singhal *et al*., 2024). It initially shows symptoms like clearing of veins, which eventually converts to vein banding. Further it shows stunting, necrosis, distortion of leaves, etc. (Meena *et al.,* 2021). Various cruciferous plants like mustard, raddish, turnip etc. are known to be infected by this virus. *Cucumber mosaic virus*, a member of genus *cucumovirus*, is a single-stranded positive sense RNA virus. It has a broad host range which shows typical virus symptoms like mosaic, leaf discoloration, yellowing of veins, leaf mottle, etc. (Shehata *et al.,* 2023).

Various reports in the recent times have suggested the co-existence of different viruses and also virus and phytoplasma together in the same host plant. Though individual infection by virus and phytoplasma has been well documented in various cruciferous crops, reports of mixed infection is still under reported. Mixed infections often complicate the accurate diagnosis of diseases due to overlap of symptoms like leaf curling, stunting, chlorosis, abnormalities in flowers.

Mixed viral infections in crucifers

Mixed infections which involve two or more plant viruses occur frequently in cruciferous vegetables. Such infections generally arise when multiple viruses share common insect vectors such as whiteflies and aphids. A phenomenon, known as viral synergism, is observed when one virus increases the symptom severity or replication of another virus (Takeshita *et al.,* 2012). In crucifers, viruses like *Cauliflower mosaic virus* (CaMV), *Cucumber mosaic virus* (CuMV) and *Turnip mosaic virus* (TuMV) have been reported to infect crops together because of their shared insect vectors (Hull, 2014). These infections lead to severe mosaic, distortion of leaf, chlorosis and eventually reduction in yield. Mixed viral infections have been reported to interfere with host defense pathways, increase viral titer in host and enhance spread of disease by increasing the transmission efficiency by their insect vectors (Xu *et al.,* 2022).

Xiao-yan *et al*. (2022) conducted a study where they collected 570 leaf samples, suspected to be infected by virus, from various crucifer crops such as *Brassica rapa* var. *pekinensis, B. oleracea* var. *botrytis, Brassica oleracea* var. *alboglbra, B. napus, Brassica oleracea* var. *capitata, Raphanus sativus, Brassica juncea, Capsella-bursa-pastoris, Brassica campestris* and *Isatis tinctoria* across many regions of China over several years. They used molecular diagnosis tools such as RT-PCR and multiplex RT-PCR using virus specific primers to identify and differentiate between *brassica yellows virus* (BrYV) genotypes and *turnip mosaic virus* (TuMV) and *cucumber mosaic virus* (CMV). They reported that BrYV was widely prevalent in China with an average incidence of 17%. TuMV and CMV was found to have higher incidence of 79.1 and 55.6 per cent respectively. Multiplex RT-PCR showed that three BrYV genotypes were prevalent as both single and mixed infections, with mixed infections occurring at a disease incidence of 38.1 per cent by more than two viral genotypes and 8.2 per cent by more than three viral genotypes. Likewise, Spence *et al.* (2002) conducted an experiment where they used *Turnip mosaic virus* (TuMV), *Cauliflower mosaic virus* (CaMV), *Beet*

mosaic virus (BtMV) to study their effect on cabbage, kale and swiss chard in controlled screenhouse experiments. The results showed that TuMV was more devastating to cabbage in compared to CaMV. Mixed infection of both the viruses reduced the marketability of cabbage by 25 per cent. They also observed that TuMV was less damaging to kale in compared to cabbage. In Swiss chards, BtMV reduced the quality and yield of leaf. This study mainly highlights the devastating effects of mixed infections in crucifers. Hunter *et al.* (2007) performed mechanical inoculation and transmission studies using aphids to study the effect of *Turnip mosaic virus, Cauliflower mosaic virus* and *Beet western yellows virus* on stored cabbage. They found that CaMV alone did not have devastating effects but the symptom expression was greatly enhanced in mixed infection with TuMV. The interactions between viruses showed variation in the sense that CaMV increased the necrosis symptom of TuMV while BWYV reduced that symptom and increased tip burn symptom. Sevik (2016) conducted a study where a total of 535 leaf samples were collected from both symptomatic and asymptomatic cabbage plants in major cabbage growing areas of Black Sea region of Turkey. The samples were tested for TuMV, CaMV, CMV, TYMV BWYV using DAS ELISA. Biological assays were also conducted by mechanically inoculating sap from infected plants into indicator hosts to study symptom development. They reported that TuMV infection was highest (8.1%), followed by CaMV (6.9%). Mixed infection of the two viruses occurred in 2.9% of samples. Other tested viruses were not present. Ayyaz *et al.* (2018) conducted a study in major cabbage growing districts of Turkey. Altogether 386 cabbage leaf samples showing typical viral symptoms were collected and tested for seven viruses namely, TuMV, CaMV, TSWV, TYMV, RaMV, BWYV and CMV. They reported that 86 out of 386 samples were infected by viruses. TuMV was the highest (11.91%), followed by CaMV (8.80%). No other viruses were present. Mixed infection of TuMV and CaMV was found to be 1.03 per cent. This demonstrated the complexity of virus-virus interaction and importance of considering the mixed viral infections in understanding disease development and yield losses of crops.

It is interesting to note that cruciferous weed species also harbour various plant viruses and aid in their survival and spread to crop plants. A study was conducted by Kyrychenko *et al.* (2023) to identify the presence of important plant viruses, namely *Cucumber mosaic virus* (CMV), *Turnip mosaic virus* (TuMV), *Turnip yellow mosaic virus* (TYMV), *Watermelon mosaic virus* II (WMV) and *Turnip crinkle virus* (TCV) in the Garlic mustard plants in Ukraine. Systematic field sampling was collected across many regions and seasons. Serological detection was done by ELISA, molecular confirmation by RT-PCR and transmission electron microscopy was adopted to strengthen the reliability of identification of selected viruses. The results showed that the garlic mustard plants were infected by *Cucumber mosaic virus* and *Turnip mosaic virus.* CMV was detected in about 80 per cent of the tested samples. TuMV was detected both independently also in mixed infection with CMV. Mixed infections of both the viruses increased the accumulation of CMV, which suggest the presence of synergistic effects among the two viruses. The other viruses which were tested were not detected. The study highlights garlic mustard as an important reservoir of these two plant viruses. Slavikova *et al.* (2022) conducted an experiment where they collected plant samples from oilseed rape fields which included oilseed rape plants, some intercrops and some weed species. The presence of turnip yellows virus (TuYV) was detected by RT-PCR using specific primers. They reported that total 160 out of 417 tested plant samples were infected by TuYV, where 23 were weed species. Moreover, High-throughput sequencing of *Papaver rhoeas* revealed that TuYV was present in mixed infection with CMV and TuMV. This study highlights the role of weed species as important reservoir of various plant viruses, sometimes present in mixed infections.

Mixed infection of virus and phytoplasma in crucifers

Co-infection by viruses and phytoplasma has been reported to be a significant and increasingly common phenomenon in crucifers. Various phloem feeding insect vectors are often shared by these pathogens which facilitate their spread to their host plants. These co-infections often produce a combination of disease symptoms such as chlorosis and mosaic, in addition to phytoplasma induced symptoms such as witches' broom, phyllody etc. (Rao *et al.*, 2017). Some reports suggest that co-infection by viruses and phytoplasma lead to synergistic effects which manifests as increased pathogen load, faster disease progression and more severe symptoms like yellowing, stunting, phyllody, witches' broom etc. (Yu and Wei, 2025). Phytoplasmas can manipulate host cellular functions by using effector proteins that affect the plant development and immune responses that make the plant more susceptible to viral infection (Drcelic *et al*., 2024). Various studies have demonstrated that mixed infections are common phenomenon in areas of intense cultivation and high vector population (Yu and Wei, 2025). Music *et al*.

(2014) collected symptomatic and asymptomatic plants of oilseed rape and used serological, biological and molecular techniques to detect the presence of viral and phytoplasma infection. Phytoplasma was detected using PCR, nested PCR and RFLP analysis of the 16S rRNA gene, followed by phylogenetic analyses and sequencing. Multilocus sequence analysis of several genes (tufB, secY, groEL and amp) was done to get a deeper understanding. Host inoculation assays, immuno-diffusion tests and full genome sequencing of *Turnip mosaic virus* (TuMV) were conducted for the purpose of virus detection. They reported the mixed infection of 'Candidatus Phytoplasma asteris' (16SrI-B sub group) with TuMV.

In mixed infections, the overlap of ecological habitats and modes of spread make the pathogens co-exist together in the same plant. Mixed infections impose heavy physiological stress on the host than single infection by disrupting photosynthesis, changing carbohydrate mechanism and impairing nutrient transport (Yu and Wei, 2025).

Epidemiology of mixed infections in crucifers

The epidemiological significance of mixed infections is shaped by several aspects such as vector overlap (sharing similar insect vectors), presence of reservoir hosts (like weed and other plants that carry the pathogens) and the pathogens that are involved, influencing the occurrence and prevalence of mixed infections in crop plants (Singhal *et al.,* 2020). These reservoir plants serve as important source of inoculum and facilitate in spread of diseases. Since the insect vectors share a common feeding habitat and existence in the same ecosystem, they facilitate the occurrence of mixed infections. Simultaneous feeding by multiple vectors in the same host and sequencial feeding on different hosts can both bring about mixed infection (Yu and Wei, 2025). Both viruses and phytoplasmas have a wide host range, which significantly contribute to their epidemiology. The cruciferous crops serve as primary sources of inoculum for the disease. Various weeds and wild plants harbour the pathogens during off seasons and serve as secondary sources of inoculum, without showing typical symptoms. Change in climate and rising temperature has led to changes in insect vector dynamics, reproduction rates and susceptibility of the hosts (Sahu *et al.,* 2026). Moreover, multiple cropping systems and continuous cropping makes the inoculum available for a longer time to infect crops. Large scale monoculture of crucifer crops facilitates vector spread and faster disease progression. Mixed cropping with other vegetables also facilitates co-infection between pathogens since it brings about shared vector populations. Therefore, as a result of such epidemiological influences, mixed infections show various implications such as increase in disease severity, enhanced vector transmission, more yield losses.

Detection and Diagnosis

Accurate diagnosis of mixed infections in crucifers is essential for effective management. But, these mixed infection of viruses and phytoplasmas cause significant complications in the epidemiology and management. Since there occurs overlap in symptoms of viruses and phytoplasmas, traditional diagnosis methods tend to be unreliable. These type of symptom based diagnosis may lead to misidentification of the disease. Various diagnostic tools such as ELISA, Real Time PCR, Multiplex PCR, and next generation sequencing has significantly facilitated the detection of such mixed infections. ELISA is mainly in use because of its simplicity and cost effectiveness, which has greatly improved the accuracy of plant virus detection (Sharma *et al.,* 2021). PCR helps in accurately detecting viruses and also in targeting the 16Sr gene to detect Phytoplasmas, which is a conserved region (Bertaccini *et al*., 2019; Abou-Jawdah *et al.,* 2018). RT-PCR also helps to convert viral RNA into cDNA to enable amplification of virus specific sequences. Various RNA viruses have been detected using this technique (Drygin *et al*., 2012; Lopez *et al.,* 2009). Multiplex PCR make simultaneous identification of various pathogens possible thereby giving a more detailed understanding of the disease complexes (Huang *et al.,* 2023, Rao, 2021). It uses multiple sets of gene specific primers in the PCR reaction mixture to simultaneously detect various pathogens (Sharma *et al.,* 2021; Lopez *et al.,* 2009). In addition to these, some advanced diagnosis tools are used to detect such mixed infections with enhanced accuracy and speed. Loop Mediated Isothermal Amplication (LAMP) is one such technology which is rapid and successfully used in detection of Phytoplasma (Muttappagol *et al.,* 2024) CRISPR based technologies also provide high specificity and detection within minutes (Li *et al.,* 2024). This enables accurate and quick detection of pathogens in mixed infection. Next generation sequencing is used for unbiased detection of all the pathogens in mixed infection. It helps in diagnosis of new and known pathogens with high resolution in genomic information (Singhal *et al.,* 2020). Multilocation sequence analysis (MLSA) improves phytoplasma detection by analyzing multiple genes. It is more useful in detection of closely related strains.

Conclusion

The plant disease etiology is no longer a simple narrative of one disease, one pathogen and instead it has evolved into something more complex where different types of pathogens coexist, interact with each other, and determine the overall health and productivity of crops. These mixed infections operate beneath the surface of traditional diagnosis methods and significantly reduce the quality and yield of produce. In crucifers, the co-existence of various viruses together and also the virus and phytoplasma together has created a biological synergy, which is both destructive and complicated. What appears as a routine yellowing or stunting, may actually be the interplay of various pathogens together. Mixed infections are often overlooked but they critically challenge the productivity and yield of crops. These interactions blur the boundaries between disease cycles of individual pathogen and ultimately convert into a more dynamic pathosystem. Therefore, the challenge lies in unravelling these complex pathogens and translating them into practical management strategies. The opportunity present here is to redefine plant disease research through the eyes of pathobiome concept. Here understanding of these infections is as essential as identifying the pathogens in the infections. Future research should focus on holistic, interdisciplinary approach which combines epidemiology, vector biology, molecular biology and climate factors. This will help in development of innovative and sustainable solutions that be effective in addressing the realities of modern agriculture. Overall, recognizing and addressing mixed infections is not just about improving crop protection. It is about aligning Plant Pathology with the true complexities of nature, where interactions not isolation define the system. Understanding these interactions will be essential to develop sustainable crop protection strategies and improving productivity in cruciferous crops.

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