Mini Review

Beneficial Plant Virus Interactions in Horticultural Crops: Emerging Roles in Stress Tolerance and Sustainable Agriculture

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Abstract | Plant viruses have historically been seen as pathogens that cause damage to plants and have been responsible for enormous economic losses in horticultural crop production worldwide. Nevertheless, an increasing body of literature is beginning to contradict this narrow view. Some plant-virus interactions can be either conditionally or always beneficial to the plant, offering advantages such as improved abiotic stress tolerance (such as drought, heat, and salinity stress); resistance to pathogens with mild strain cross-protection; and altered relationships with insect vectors, which might result in reduced disease spread. This study provide an overview of our current understanding of beneficial plant virus interactions in horticulture, with a focus on three main areas: (i) tolerance to abiotic stress, achieved through ABA signaling, osmolytes, and metabolism alteration; (ii) biotic stress resistance using mild strain cross-protection, a technique with documented commercial success for citrus, tomato, papaya, and cucurbit production; and (iii) recent findings about plant-virus tri-trophic interactions, which involve attraction of natural enemies and deterring of insect vectors. The current study aims to examine these mechanisms in detail, focusing specifically on salicylic acid signaling, RNA interference regulation, and detoxification of reactive oxygen species. In addition to its effectiveness in managing citrus diseases, the four-decade track record of Citrus tristeza virus-mediated protection against plant pathogens provides proof of concept that virus management and not elimination is feasible. At the same time, substantial issues remain, such as strain instability, regulatory concerns, and situational dependency of positive outcomes. The proposed research priorities seek to transform the "viruses as friends" paradigm into a reality.

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Introduction

Plant viruses are a significant economic factor in world horticulture, causing economic damages amounting to more than US$30 billion annually in vegetable, fruit, ornamental, and other specialized crops (Agrios, 2005; Hull, 2014). The prevailing model within plant virology for years has been one in which viruses are considered obligate parasites that reproduce through the exploitation of host cell

resources, leading to defensive responses that redirect metabolic energies away from plant development and propagation, often culminating in symptoms such as chlorosis, necrosis, or mosaics, resulting in decreased yields and reduced marketability (Gao and Lozano-Durán, 2025).

The emergence of a paradigm shift is now well underway. Evidence gathered from studies in field ecology, large-scale metagenomics experiments, and experimental model systems suggests that the nature of virus-plant interactions spans a wide range, including acute pathogenesis but also commensalism, latent infection, and even true mutualism (Wren *et al*., 2006). Roossinck (2011) made an important contribution with a review article that highlights "good viruses" that form symbiotic relationships with plants, with benefits like increased abiotic stress resistance, improved defense against pathogens, and changes in relationships with insect vectors and herbivores.

The complexity of the interactions between viruses and plants in horticulture systems is of utmost importance due to the nature of intensive cultivation practices in such systems, which contribute to quick virus transmission through methods like dense planting, irrigation, and exchange of propagating material throughout the world (Rubio *et al*., 2020). In addition, there are increasing threats to the health of these crops through climate change in the form of more droughts, heatwaves, and salt stress associated with irrigated farming systems, alongside increased limitations imposed on artificial pesticides and increased demands from consumers for sustainable produce (FAO, 2022).

The main application of good viral biology in agriculture is mild strain cross-protection, which involves the purposeful infection of the host with a harmless strain of the virus to protect against a harmful strain of the same virus. The use of cross-protection was first reported by McKinney (1929) using Tobacco mosaic virus on tobacco plants. Cross protection is used as a commercial practice in citrus crops against Citrus tristeza virus in Brazil (Costa, 1980); in tomatoes against Tomato mosaic virus in Europe and Japan in glasshouses (Rast, 1972); and in papayas against Papaya ringspot virus in Taiwan (Yeh, 1988). Apart from cross-protection, the finding that infection with Cucumber mosaic virus causes improved drought resistance in tobacco and tomato (Xu *et al*., 2008) and that there exists a three-way mutualism of a tropical grass, an endophytic fungus, and a mycovirus that together allow survival in geothermal soils (Márquez *et al*., 2007) has revolutionized our understanding of virus-host interaction.

In this paper, the current knowledge on the topic of positive plant-virus interactions in horticultural plants is gathered, focusing on stress tolerance, molecular mechanisms involved in the processes, and practical aspects of sustainable horticulture. This review presents the categorization of beneficial interactions, analysis of reported examples of such interactions in horticulturally significant crops, as well as issues associated with further development of this quickly expanding area. Tables 1-3 and Figure 1 present summarized data concerning documented beneficial interactions, molecular mechanisms of interaction, and timeline of significant events in this field.

Beneficial virus–plant interactions: Classification and ecological context

Symbiotic relationships between viruses and plants can be classified based on two major aspects: reliability and scale of the advantage, and the way that it is achieved. According to Roossinck and Bazan (2017), three types of symbiosis exist between plants and their viral partners: Mutualism, commensalism, and conditional mutualism. Mutualism is when the virus increases plant fitness under certain conditions consistently; one example of such an interaction would be the thermal tolerance symbiosis described by Márquez *et al*. (2007), where the mycovirus becomes indispensable in geothermal soils warmer than 38 °C. In commensalism, the viral infection occurs without affecting the health of the host; such viruses have been found quite commonly using metagenomic surveys of viral infections in plants. Finally, conditional mutualism, which might be the most agriculturally significant type of relationship, occurs when the benefits from the infection emerge only during the exposure of the host to some form of stress, as evidenced in CMV-induced drought resistance (Xu *et al*., 2008).

One of the critical ecological principles that shapes this paradigm shift is the surprising frequency of persistent viruses in natural and agricultural ecosystems of plants. According to Roossinck (2015), in viral metagenomics studies conducted in plants from different families, it was observed that a considerable number of viruses possess persistent and vertically

transmitted life cycles and do not require insects for transmission; instead, viruses get transferred through seeds and pollen. They belong to the viral families like Partitiviridae, Endornaviridae, as well as some novel families. It can be argued that these persistent viruses seem to be a million-year-old association that has evolved alongside their host plants and does not cause any harm.

In agriculture, domestication and improvements in varieties apply selection pressure on the virome of plants, which has affected the composition of the virome in unpredictable ways. Selection by humans based on visually healthy, highly productive phenotypes may have inadvertently removed some beneficial virus infections from their repertoire of interactions, while virus resistance genes introduced through breeding practices may have altered the balance of ecosystems in terms of viruses within the plants (Takahashi *et al.*, 2019). Table 1 shows examples of beneficial interactions between plants and viruses in different horticulture crops.

Virus-mediated abiotic stress tolerance

Drought tolerance: The most rigorously characterized example of virus-mediated abiotic stress tolerance in plants is the enhancement of drought tolerance by CMV, documented by Xu *et al.* (2008) in a landmark study that continues to define the field. The progressive water withdrawal rates had significantly longer drought periods than uninfected Nicotiana benthamiana and tomato plants, as well as reduced wilting index, and maintained stomatal control and recovery after re-watering. Upcoming found abscisic acid (ABA), a key player in drought stress signaling, to be produced in greater amounts, proline as the compatible osmolyte to accumulate, dehydrins and late embryogenesis abundant (LEA) proteins to be up-regulated, and general metabolic reprogramming resulting in high levels of stress-protective γ-aminobutyric acid (GABA) and from polyamine accumulation (Gechev *et al.*, 2012). Importantly, this drought tolerance phenotype was virus-strain-specific; some CMV isolates provided high levels of drought tolerance, whereas others were virus isolates that caused typical pathogen-related symptoms but provided no drought tolerance, highlighting that the positive impact of the genetic trait is specific to certain virus genotypes and is not inevitably the result of CMV infection (Bergès *et al.*, 2020).

Table 1: *Representative examples of beneficial plant–virus interactions in horticultural crops.*

Virus (Abbreviation)	Host crop (s)	Benefit type	Key findings	Key reference(s)
Cucumber mosaic virus (CMV)	Tobacco, Tomato, Pepper	Drought tolerance; insect vector repellence	Elevated ABA and proline; osmolyte accumulation; repellence of alate aphids via VOC changes; attraction of parasitoid wasps	Xu *et al.* (2008); Ziebell *et al.* (2011)
Citrus tristeza virus (CTV) mild strains	Sweet orange, Grapefruit, Lemon	Cross-protection against virulent CTV (quick decline, stem pitting)	>70–90% reduction in disease incidence in multi-year field trials; commercial practice >40 years in Brazil and USA	Costa (1980); Moreno *et al.* (2008)
Papaya ringspot virus (PRSV) mild strain HA 5-1	Papaya	Cross-protection against yield-devastating PRSV strains	>85% protection under high inoculum pressure; foundational for subsequent transgenic resistance approach	Yeh (1988)
Tomato mosaic virus (ToMV) attenuated strain MII-16 (L11A)	Tomato (glasshouse)	Cross-protection against virulent ToMV; no chemical residues	80–95% efficacy; standard commercial practice in Dutch and Japanese glasshouses for >50 years	Rast (1972)
Zucchini yellow mosaic virus (ZYMV) mild strain ZYMV-WK	Zucchini, Cucumber, Squash	Cross-protection against virulent ZYMV	60–80% reduction in mosaic/stunting symptoms; registered as biocontrol product in France and Israel	Lecoq (1991)
Curvularia thermal tolerance virus (CThTV)	Dichanthelium lanuginosum (via Curvularia protuberata endophyte)	Thermal tolerance: survival in geothermal soils >38°C	Obligate three-way mutualism; virus curing abolished thermal tolerance in both fungus and plant	Márquez *et al.* (2007)
Tobacco mosaic virus (TMV) mild strains	Tobacco, Tomato	Cross-protection; priming of SA-mediated SAR	Historical model system; SA-mediated systemic acquired resistance induction documented; first cross-protection report	McKinney (1929); Sherwood and Fulton (1982)
Watermelon mosaic virus (WMV) mild strain	Watermelon, Melon	Cross-protection against virulent WMV strains	Reduced mosaic and yield losses in field trials; strain-specific protection efficiency	Gonsalves and Fulton (1987)

Subsequent studies have focused on analyzing the effects of drought resistance in other horticulture host virus combinations. For example, when peppers (*Capsicum annuum*) are infected with the virus (CMV), they exhibit greater resistance to moderate levels of water scarcity in terms of improved water use efficiency, leaf wilting, and maintenance of photosynthesis capacity in comparison with non-infected plants (Pagán *et al.*, 2014). The dependence on cultivar is particularly significant for future agricultural applications, as it means that the beneficial effect can be cultivar-specific. Therefore, more research needs to be done before introducing the strain to certain cultivars in order to ensure the expected results.

Heat and thermal tolerance

One of the best examples of viruses conferring heat tolerance on their hosts involves the remarkable symbiotic relationship involving a fungus, its associated mycovirus, and a higher organism, detailed by Márquez *et al.* (2007) at Yellowstone National Park in geothermal areas. The tropical panic grass *Dichanthelium lanuginosum* can survive soils with temperature levels above 65°C but only as long as it is associated with an ascomycete endophyte, Curvularia protuberata, which must be infected with the Curvularia thermal tolerance virus (CThTV), a double-stranded RNA mycovirus of the Totiviridae family. Removal of the virus from the fungal symbiont using a dsRNA-degrading antiviral agent resulted in irreversible loss of heat tolerance not only of the fungus but also of the plant itself. Subsequent re-infection of the fungi with (CThTV), reestablished heat tolerance of the fungi as well as the plants they were associated with. Virus-induced thermotolerance within the context of direct colonial horticultural systems is an emerging area that continues to develop slowly. There have been cases where plants infected with tobamoviruses maintain heat shock protein expression during high temperatures compared to non-infected plants (Hull, 2014). It seems possible that the infection acts as a primer of sorts that could be useful in managing heat stress.

Salinity and osmotic stress tolerance

Viral influence on salt resistance in crop plants has been less well studied compared to the influence of drought or heat stress; however, the body of literature seems to indicate that viruses play a role in regulating ionic balance and osmoregulation. Tobamoviruses have been shown to positively affect the K^+/Na^+ ratio and reduce electrolyte leakage in the presence of NaCl. The effect seems to be mediated through a virus-induced response, specifically involving the production of salicylic acid (SA), which regulates ion transport gene expression (Hull, 2014; Roossinck, 2011). Even though these observations provide correlations, demonstrating causation between ionic resistance and metabolism requires additional experimentation.

Cold and frost tolerance

Cold tolerance, as a phenotype mediated by viruses in plants, is by far the least studied of the abiotic stress categories. Molecular pathways involved in cold acclimation and plant defense against pathogens share many regulatory checkpoints, including interactions among salicylic acid (SA), jasmonic acid (JA), and C-repeat element-binding factors (CBFs). Cold acclimation can be induced by viruses causing constitutive activation of SA signaling pathways; however, no empirical evidence has been provided in the case of horticultural plants as yet (Verma *et al.*, 2016). Table 2 below highlights the available data about virus-induced abiotic stress tolerance and the proportion of various effect categories described in scientific studies.

Virus-induced resistance to biotic stresses: Cross-protection and tri-trophic effects

Cross-protection stands out as the most ancient, best understood in terms of its mechanisms, and most commercially utilized example of virus–plant associations in gardening. First discovered by McKinney (1929), who found that tobacco plants infected with a mild strain of tobacco mosaic virus (TMV) were immune to further attacks with a virulent strain, cross-protection has since been observed in many diverse virus-host systems and commercially applied to several crop plants. The underlying mechanisms can be classified as including, at least, two non-exclusive modes: (i) RNA silencing-induced immunity, where siRNAs originating from the mild strain silence homologous genes in the challenging virulent strain (Ding and Voinnet, 2007; Voinnet, 2001); and (ii) coat protein interference, where the coat protein of the mild strain blocks cell-to-cell transport and/or uncoating of the attacking virulent strain (Sherwood and Fulton, 1982; Beachy, 1999). Depending on the viral host pairs, the contribution of one or another of the mechanisms varies, depending on the genetic relatedness of the mild and virulent strains.

Table 2: *Documented cases of virus-mediated abiotic stress tolerance in plants relevant to horticultural crops. ABA, abscisic acid; GABA, γ-aminobutyric acid; ROS, reactive oxygen species; SA, salicylic acid; SOD, superoxide dismutase; CAT, catalase; dsRNA, double-stranded RNA.*

Virus	Host	Stress type	Documented physiological response	Proposed molecular mechanism	Reference
CMV	N. benthamiana, Tomato	Drought	ABA signaling ↑; stomatal closure ↑; proline ↑; dehydrin expression ↑; improved survival at −50% field capacity	ABA-dependent stress signaling; metabolome reprogramming GABA ↑ and polyamines ↑	Xu *et al.* (2008)
CMV	Pepper (C. annuum)	Drought	Improved water use efficiency under moderate deficit; cultivar-dependent benefit	ABA-mediated stomatal regulation; strain-specific metabolic induction	Pagán *et al.* (2014)
CThTV (in Curvularia fungal host)	Dichanthelium lanuginosum (tropical panic grass)	Heat (>38°C)	Survival in geothermal soils; metabolite reprogramming at fungal–plant interface; obligate tripartite requirement	Indirect: mycovirus modulates fungal secondary metabolism to confer thermal protection	Márquez *et al.* (2007)
TMV mild strains	Tobacco, Tomato	Salinity	Maintenance of K^+/Na^+ ratios; reduced electrolyte leakage; sustained photosynthesis under NaCl stress	SA-mediated ionic homeostasis; upregulation of ion transporter genes via defense cross-talk	Hull (2014); Roossinck (2011)
Beet curly top virus (BCTV)	Tomato, Bean, Beet	Drought/ Heat	Reduced transpiration; cuticle thickening; modified stomatal density in infected leaves	ABA pathway activation; symptom-related phenotypic changes incidentally reduce water loss	Agrios (2005)
CMV attenuated strains	Tomato	Heat stress	Reduced ROS accumulation; enhanced antioxidant enzyme activity (SOD ↑, CAT ↑)	Priming of antioxidant defense via virus-triggered SA and ROS signaling cross-talk	Hull (2014)
Tobacco rattle virus (TRV) VIGS vector	Multiple crops (experimental)	Multiple	Used as a VIGS tool to identify stress-tolerance genes; tolerance phenotypes validated by gene silencing	Virus-induced gene silencing (VIGS) as an experimental tool; stress-tolerance associations incidental	Roossinck and Bazan (2017)

The use of mild strains of Citrus tristeza virus (CTV) to provide cross-protection of citrus crops against viral disease in Brazil exemplifies a highly successful case of biological disease control on an industrial scale. CTV is a virus causing two economically devastating diseases in citrus, the rapid decline of sweet oranges grown on sour orange rootstock and the stem pitting of grapefruits and sweet oranges grown on resistant rootstock. It had already decimated tens of millions of citrus trees in Brazil by the 1940s. The application of CTV mild strain cross-protection to protect sweet oranges from rapid decline through pre-immunization was accomplished by Costa (1980), who showed a >75% reduction in rapid decline incidence using mild CTV strains after several years of trials, and this method has been applied commercially for over four decades (Moreno *et al.*, 2008).

In the case of papaya, for instance, the work of Yeh (1988) established the fact that cross-protection induced by relatively mild PRSV variants successfully protected papaya from yield-sapping PRSV variants under heavy inoculum pressure in Taiwan, with success rates of more than 85%. This was crucial in providing insights into further developments in genetically engineered PRSV resistance utilizing the coat proteins (Tepfer, 2002).

Cross protection using the weakened strain of Tomato mosaic virus (ToMV), known as strain MII-16, in which the process was first demonstrated by Rast (1972), developed into the normative practice in the Netherlands and Japan among glasshouses. This approach was consistently applied using either dipping the tomato plantlets or stem inoculation before planting the seedlings in the field. This method provided between 80-95% immunity from virulent strains of ToMV at negligible costs with no chemical residue and became an integral part of ToMV control strategies for many years until the use of the Tm-2 and Tm-2^2 resistance genes in tomatoes.

In addition to classical cross-protection, virus-mediated indirect biotic resistance via manipulation of plant-insect interactions has also been documented. The study by Ziebell *et al.* (2011) showed that CMV infection and the 2b RNA silencing suppressor protein of the virus can alter the composition of

Table 3: *Commercial and semi-commercial applications of mild-strain cross-protection in horticultural crops.*

Target virus	Crop	Region/ Country	Mild/Attenuated strain	Protection efficacy	Commercial status
CTV (quick decline and stem pitting strains)	Sweet orange, Grapefruit	Brazil, USA, Spain	Naturally selected mild CTV field isolates (pre-immunization)	70–90%	Commercially deployed >40 years; industry standard in Brazil
PRSV	Papaya	Taiwan, Hawaii (USA)	Mild strain HA 5-1; subsequently replaced by the transgenic CP approach	80–90%	Commercial in Taiwan; transgenic in Hawaii
ToMV	Tomato (protected cultivation)	Netherlands, Japan, Israel	MII-16 / L11A attenuated strain	80–95%	Routine commercial practice in glasshouses >50 years
ZYMV	Zucchini, Cucumber	France, Israel	ZYMV-WK mild strain	60–80%	Registered biocontrol product; semi-commercial use
CMV (P-strain)	Pepper	South Korea, Japan	CMV-P mild isolate	50–75%	Limited commercial use; largely at the research stage
WMV	Watermelon, Melon	USA, Mediterranean	WMV mild field isolates	50–70%	Field-tested; no formal registration; farmer-managed in some areas
TSWV	Tomato, Pepper	Worldwide (experimental)	Defective interfering RNA strategies (experimental)	40–60%	Pre-commercial; regulatory evaluation pending

VOCs significantly in tobacco in such a way that they strongly repel alate aphids – main carriers of CMV, while at the same time attract parasitoid wasps that are aphid predators. This three-tiered interaction, whereby the virus manipulates plant chemistry to repel its carrier insect and attracts predators of said vector is an excellent illustration of virus-mediated indirect biological control. The following Table 3 illustrates some applications of cross protection in commercial and semi-commercial settings.

Molecular mechanisms underlying beneficial viral effects

Molecular structures involved in virus-plant symbiosis include several signaling pathways that overlap significantly with the existing stress responses and defense mechanisms. One of the key molecules in this structure is salicylic acid (SA). An SA buildup marks the plant's response to biotrophic pathogen infection and acts as an initiating factor of SAR, a general form of disease resistance that protects against further damage from pathogens. Many infections with viruses that increase plant resistance to biotic stresses occur via sustained but minimal SA signaling to induce SAR without incurring the costs of growth inhibition that would be incurred from excessive buildup of SA (Murphy *et al*., 2020). It should be noted that SA signaling crosstalks with abiotic stress response: Increased SA levels can have an effect on stomatal conductance and activities of ion transporters and antioxidants. The second key element of the mechanism is RNA silencing. In plant cells, dsRNA-mediated action of the RdRp enzyme leads to several small RNA-mediated mechanisms, namely, siRNA and microRNA (miRNA) mechanisms, responsible for degrading viral RNA as well as controlling gene expression in host organisms (Pandey *et al*., 2008). As for cross-protection, siRNAs developed against the mild form contribute to creating a state of resistance, which will prove efficient to some degree against aggressive forms, provided that there is significant sequence similarity between the two forms of infection. Apart from cross-protection, RNA silencing provoked by low-level viral replication can result in the development of secondary siRNAs, affecting the natural stress response of plants in a way different from direct protein actions.

Metabolic reprogramming is a way in which viruses can contribute to their hosts in three different ways. Firstly, according to Xu *et al*. (2008), in the first metabolomics study of any virus-host interaction, the metabolome of tobacco plants infected by CMV changed significantly to include higher concentrations of proline, GABA, and various polyamines known as compounds involved in osmotic regulation and membrane protection in conditions of drought, as well as a change in lipids indicating enhanced membrane stability. Secondly, these changes appear to occur as a consequence of altered transcription factors and metabolic enzymes caused by the viral infection rather than a biochemical effect of the virus itself. This would mean that the virus acts as a "metabolic modulator," altering its host to make it better able to cope with environmental stresses as an accidental outcome of

its infection. Which viral genes cause this change is still unknown, but knowing this will enable selective breeding/strain engineering in the future (DeLong *et al*., 2021).

Implications for sustainable horticulture

The concepts of sustainability, which include reducing artificial chemical inputs, increasing efficiency of resources and energy, preserving biological diversity, and maintaining ecosystems, are consistent with the attributes of good design of beneficial virus interactions (Scortichini, 2022). Mild strain cross-protection shows several sustainability-related features. These features include avoiding the necessity to repeat treatments because one initial treatment protects throughout the whole growing season, lack of residue on the produce and in the soil, compatibility with IPM programs, and safety from the biosafety standpoint due to the use of naturally existing mild strains. Forty years of commercial utilization of CTV cross-protection to protect billions of citrus plants in Brazil show that large-scale virus management is possible both technologically and financially.

The potential future use of the beneficial properties of viruses for improving the ability to tolerate abiotic stresses holds great potential for climate adaptation within horticulture. The production of plants within horticulture in areas experiencing arid, semi-arid, and drought conditions is becoming progressively difficult due to issues of lack of water supply and high temperature occurrences. If plants can be made tolerant to these environmental stresses through the introduction of these types of viruses without compromising their yields or quality, then such a strategy would provide the tools needed for creating resilient farming systems in terms of climate while reducing chemical and irrigation requirements (Roossinck, 2019).

Challenges and future perspectives

Although there is a considerable body of evidence suggesting that virus-plant interactions are indeed beneficial, several important issues need to be taken into account for such evidence to be successfully applied to practical horticultural applications. Predictability and genetic stability of the desired benefits pose serious challenges. Populations of viruses are known to be genetically diverse and highly prone to evolution due to high rates of reproduction, RNA-dependent RNA polymerases that tend to make errors during RNA replication, and frequent recombination events. It may well happen that a mild strain used for achieving cross-protection may gradually evolve towards more virulence. Therefore, continuous monitoring of such strains in field conditions should be mandatory; otherwise, the use of those strains cannot be approved according to current legislation (Tepfer, 2002).

The process of regulatory approval for artificial introductions of viral agents into agricultural environments is complex and jurisdiction-dependent, often being extremely conservative in nature. Even the most extensively studied natural, benign strains will face an extensive regulatory scrutiny that will hinder their commercialization even after decades of safe application. For the expansion of their authorization to cover new combinations of crops and virus strains, it would require intensive safety evaluation, which is not affordable by many academic or smaller commercial research projects, hence creating a major impediment from research to practice. There is a need for regulatory science to adapt in order to reflect the proportionate risks for the uses of benign strains, as the risks associated with field strains of benign viruses differ from those linked to genetically modified organisms. Finally, there are ecological risks arising from the large-scale use of beneficial viruses, which should be addressed through further scientific research (Tepfer, 2002; Roossinck, 2012).

Research priorities will be: (i) the use of next generation sequencing in metagenomic studies for the identification of naturally occurring mild and latent virus strains in different germplasms of various horticulture crops; (ii) field and green house testing to identify the environmental and genetic determinants which influence whether a particular virus-host relationship results in positive or negative consequences; (iii) metabolomic, transcriptomic and proteomic studies for identifying molecular switches which define the outcome of the virus-host relationship; (iv) field trials to assess the genetic stability and epidemiology of mild virus strains; and (v) the establishment of globally consistent risk proportional regulatory pathway systems for the management of natural mild virus strains in biocontrol applications in horticulture cropping systems. Figure 1 provides a timeline of key milestones in the discovery and commercial application of beneficial plant–virus interactions in horticulture (1929–2024). The timeline illustrates the transition from serendipitous observational

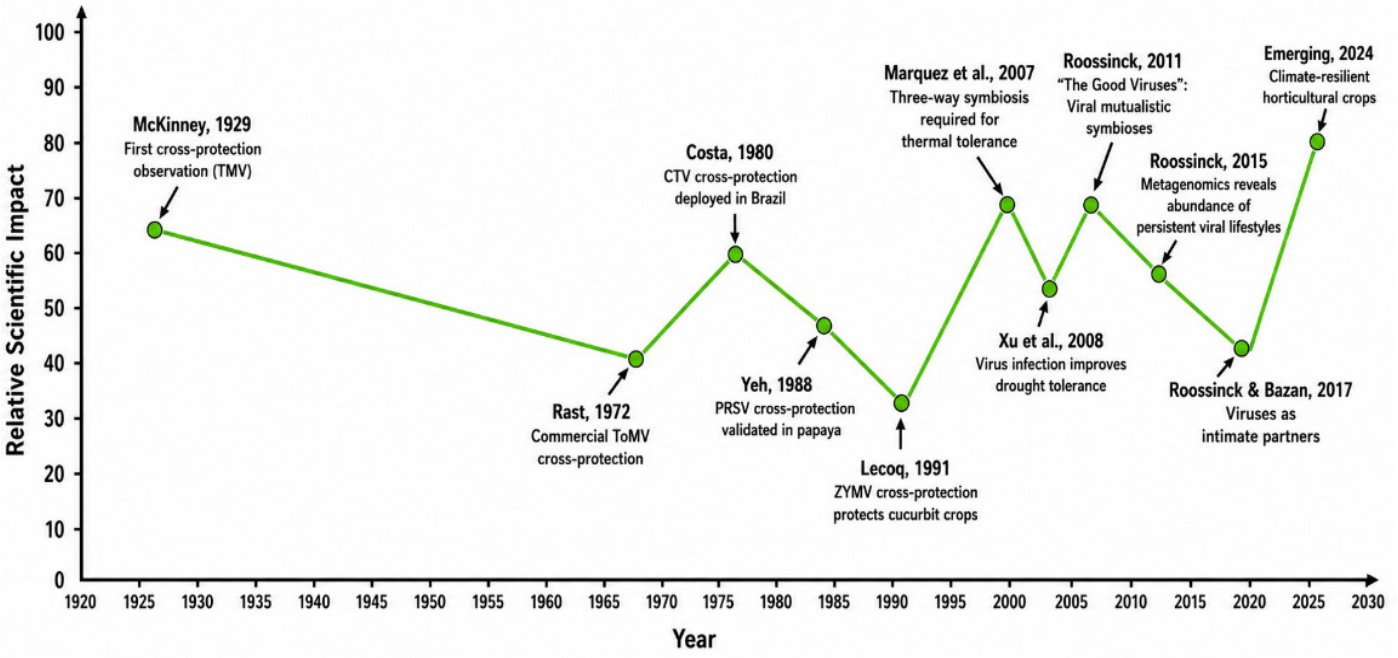

Figure 1: *Timeline of key milestones in the discovery and commercial application of beneficial plant–virus interactions in horticulture (1929–2024).*

discovery of cross-protection in the early twentieth century, through commercial deployment in major crop systems from the 1970s to 1990s, to the emergence of a mechanistic understanding of viral mutualism and abiotic stress tolerance in the 2000s and 2010s. The contemporary period is characterized by increasingly systematic, metagenomic approaches to virus discovery and by growing recognition of the potential applications of beneficial viruses in climate-adaptive, sustainable horticulture.

Conclusions

The recognition that plant viruses can function as mutualistic or conditionally beneficial partners for their hosts constitutes one of the most transformative conceptual advances in plant virology over the past two decades. In horticultural crops, where productivity, quality, and resilience must be achieved with decreasing reliance on synthetic inputs, beneficial virus–plant interactions represent a scientifically grounded and practically relevant resource for sustainable crop management. Mild-strain cross-protection has already proven its value in commercial citrus, tomato, papaya, and cucurbit production, demonstrating that deliberate virus management rather than virus eradication alone is a viable and durable agricultural strategy. The emerging evidence for virus-mediated abiotic stress tolerance, particularly drought and heat tolerance mediated through ABA signaling and metabolic reprogramming, aligns with the most urgent needs of climate-adaptive horticultural systems in an era of accelerating climate change.

Realizing the full potential of these interactions will require sustained interdisciplinary collaboration among plant virologists, ecologists, plant physiologists, agronomists, and regulatory scientists. It will also require a cultural shift in how the plant pathology community frames the virus–plant relationship, moving beyond the binary of "pathogen vs. host" toward an ecological understanding of virus–plant associations as dynamic, context-dependent partnerships shaped by evolutionary pressures and environmental conditions. As this emerging paradigm continues to mature, it promises to enrich both fundamental understanding of virus ecology and the practical toolkit available to sustainable horticultural production worldwide.

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Novelty Statement

This mini-review provides a concise, up-to-date perspective on the emerging beneficial roles of plant viruses in horticultural crops, shifting the focus from their traditional perception as pathogens to their potential as contributors to stress tolerance and sustainable agriculture. It summarizes recent evidence demonstrating how selected virus–plant interactions can enhance tolerance to abiotic stresses through physiological and molecular mechanisms. By integrating these findings with their implications for climate-resilient horticulture, this review highlights emerging opportunities, current limitations, and key research priorities, offering a fresh perspective for future research and sustainable crop management.

Generative AI and AI assisted technology statement

The author declares that no generative AI and AI assisted technology was used in the creation of this manuscript.

Conflict of interest

The authors have declared no conflict of interest.

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