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REVIEW

Tolerance of plant virus disease: Its genetic, physiological, and epidemiological significance

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Abstract

The development and use of tolerance have been proposed as an alternative or complementary method to host resistance in the management of plant diseases, including those caused by viruses. There has been much ambiguity among plant pathologists, plant breeders, and agronomists in the meaning of tolerance and how it can be operationally defined, but a modern consensus seems to have emerged. Tolerance is a relative term that means a limited reduction in host plant fitness (reproduction or survival) in relation to pathogen load throughout or during a defined period of plant development and growth such as the reproductive stage. This emphasizes the need to study reproductive stage disease tolerance. Despite this apparent consensus, there remain questions over the use of model plant systems, the genetic background of tolerance, its physiological expression, and epidemiological consequences of its deployment in crops, in comparison with host resistance. Most examples of tolerance reviewed here are for plant virus systems, although other pathogen taxa are referred to, as is tolerance as a natural phenomenon in wild plants including crop relatives. An argument is made for studying commonalities and interactions in host responses to biotic and abiotic stressors; in particular, whether virus infection can mitigate the impact of heat, cold, drought and salinity stress in plants. Finally, we review the use of mathematical models as a means of evaluating the strategy of using tolerance in disease and crop management.

KEYWORDS

abiotic stress, disease management, host plant resistance, plant reproductive fitness, vulnerability

1 | INTRODUCTION

Plant diseases present a threat to food security, plant health, and ecosystem services (Ristaino et al., 2021; Rizzo et al., 2021). Crop losses due to pests and diseases in the five major food crops (rice, maize, wheat, soybean, potato) have been estimated to range on average between 8% for potato and 30% for rice (Savary et al., 2019) but have been estimated less frequently for minor crops, those of regional importance only, or for non-food crops. The ecological

impacts of disease in natural plant ecosystems and landscapes as they affect population ecology and community structure have been reviewed (Gougherty & Davies, 2021; Jeger, 2022), but little has been done on losses in relation to the ecosystem services they provide. Plant diseases caused by viruses can be particularly damaging crops and cropping systems (Jones & Naidu, 2019). Most known plant viruses are transmitted by vectors, which acquire the virus from infected plants and inoculate the virus in healthy plants, although there is increasing recognition of the importance of seed and pollen transmission in disease epidemiology (Pagán, 2022). Vectors come from a range of insect families, although aphids, whiteflies, and other hemipterans are particularly important (Bragard et al., 2013). Transmission plays a critical part in disease epidemiology and depends to a large extent on vector life history and behavior concerning movement, landing, settling, feeding, and reproduction of plants.

Durable host plant disease resistance is perceived as the goal in disease management that would minimize the need for use of conventional plant protection chemistries. Breeding for resistance has been seen as the simplest and most effective means of avoiding crop losses from virus diseases, and as playing a major role in developing strategies for disease management (Lecoq et al., 2004). Overall, the introduction of disease resistance in cultivated plants has been made possible through conventional breeding and biotechnological approaches but these can take years to develop within a framework limited by existing knowledge, technology, and regulatory issues. Conventional breeding methods have been pivotal to obtain new plant genotypes with disease-resistant traits to withstand epidemics, with major opportunities arising with new gene editing technologies (Pixley et al., 2019). However, a practical problem arises from the time-consuming and labour-intensive demands of host phenotyping in field populations (Mahlein et al., 2019; Shakoor et al., 2017). The question remains whether resistance can be developed and implemented to manage emerging disease threats such as by targeting generic stress response rather than plant defence mechanisms, especially under the circumstances of climate change (Newton et al., 2012).

The issue of the durability of resistance is linked not only to the molecular and physiological responses to pathogen challenge but to how host resistance is deployed in crop populations. Resistance is widely recognized by plant breeders and workers in molecular host-pathogen interactions as referring to resistance genes or quantitative traits, but less in terms of how resistant cultivars should be deployed in cropping systems, which raises wider epidemiological and agronomic issues. From an evolutionary perspective, there may be constraints on the range of host genotypes a pathogen strain can adapt to, with implications for breeding for durable resistance and epidemiology (Laine & Barrès, 2013). The term 'vulnerability' may describe better the impact of pathogens on crops where there are varying environmental, agronomic, and stress factors in host plants to consider. How then to breed crops for reduced vulnerability to pathogens, does host resistance offer the best opportunity, and is there a role for tolerance—the topic of this review?

For plant virus disease, as with other pathogen groups, less attention has been given to how host resistance should be used in the field. A large body of work has been directed at the development of plants with resistance to plant viruses, combining the screening of molecular markers for genotype selection through to phenotype selection in field trials (Akhter et al., 2021; Gallois et al., 2018; Soosaar et al., 2005). However, by comparison, little has been done on the transmission and spread of plant viruses in resistant varieties under field conditions. Resistance has long been considered the major means of controlling plant virus epidemics, but some recent work has proposed tolerance as an alternative or complementary management strategy. "Tolerance as a disease management strategy has been claimed to be as widespread as host resistance although problems remain in the strict definition of tolerance and how it can be assessed" (Jeger, 2020). Tolerance has been defined as a limited symptom development or reduction in plant vigor or yield despite a normal virus accumulation as in a susceptible cultivar, or alternatively as a limited reduction in plant fitness (survival, fecundity, reproduction period), whereas for a resistant variety, there is limited virus accumulation and symptom development but a possible penalty in terms of reduced vigor and yield. Developments in the concept of tolerance are reviewed and whether it offers better opportunities for reducing vulnerability to plant pathogens. How tolerance is currently viewed from genetic, physiological, and epidemiological perspectives, in relation to plant viruses and other pathogens of crops and wild plant populations, is introduced. Finally, the limited field studies on tolerance and the potential contribution to be made by mathematical models in developing disease management strategies are assessed.

2 | DEVELOPMENTS IN THE CONCEPT OF TOLERANCE IN PLANT PATHOLOGY

2.1 | Terminology

Terminology is not solely a matter for pedants, it can be critical in avoiding ambiguity and misunderstanding in usage. There are inherent dangers in adopting terms used in everyday language and using them in a physical or

biological context. For example, resistance is a measure of the opposition to current flow in an electrical circuit and is measured in physical units of ohms. When used in the context of the plant response to challenge from a pathogen, further terms are used to clarify the meaning, ranging from immunity to partial susceptibility, the restricted and relative ability to infect, colonise and multiply in a host plant. There is no unambiguous definition as in the physical usage. The terms tolerance and sensitivity have definitions in everyday use to describe aspects of human behavior, typically tolerance is the willingness to accept beliefs that are different from your own, although you might not agree with them, whereas sensitivity is the ability to understand what people need and be helpful to them. Hence, it is possible to have the combinations: tolerant and sensitive, tolerant but insensitive, intolerant but sensitive, and intolerant and insensitive. In engineering, tolerance refers to the amount by which a measurement or calculation might change and still be acceptable—the permissible limit of variation, whereas sensitivity is the smallest absolute amount of change that can be detected by a measurement. Hence, there is a complete dependence of the two terms on each other. In statistics, tolerance refers to the statistical interval within which at a given confidence level a specified proportion of a sampled population falls, whereas sensitivity is the proportion of cases with a defined condition that are correctly identified as having the condition—the true positive rate. The two terms are combined in a single usage as tolerance sensitivity analysis in linear programming (Wendell, 2004). For host–pathogen systems, sensitivity is often used as the antonym of tolerance, or at least with each term representing the opposites of a relative scale for the host response.

2.2 | Historical developments

The first formal definition of tolerance in the plant pathology literature was made by Schafer (1971) following work dating back to the late 19th century, notably with cereal leaf rusts. Schafer (1971) considered tolerance to fall within the broad umbrella concept of disease resistance as including the following: (a) escape, (b) exclusion, (c) host–parasite interactions following infection, which leads to differing levels of disease, and (d) tolerance or endurance of a given level of disease. In this sense, tolerance means that "plants endure severe disease without severe losses in yield or quality." Tolerance can only occur when loss or damage is not a direct function of disease severity and can only be measured, by reference to its absence, when there is equivalent severity of disease without equivalent damage or loss. This definition potentially transforms a qualitative concept into one that can be operationally defined by the concept of equivalence. When disease resistance is restricted to the narrow sense of (c) above, this provides a clear distinction from tolerance viewed as somewhat intermediate between immunity and full susceptibility. Schafer (1971) also pointed out that with plant viruses, the confusion in usage of the term tolerance, at that time, was more apparent than for other pathogens, recognising that direct assessments of virus titre can be made rather than visual assessment of disease severity typically as made for the cereal leaf rust diseases. It can be argued that such confusion has persisted until today.

Cooper and Jones (1983) expanded the discussion for plant viruses. In a broader discussion of the terms used to describe plant responses to viruses. They considered it would be useful to reserve the terms resistant and susceptible to denote the opposite ends of a scale representing the effects of a host plant on virus infection, multiplication, and invasion, whereas tolerant and sensitive denote the opposite ends of a scale representing the disease reaction of the host plant to virus infection and establishment. According to the authors, tolerance describes a host that a virus can infect, replicate, and invade without leading to severe symptoms or diminishing plant growth or marketable yield. Plants can be resistant to the virus and tolerant to the disease.

The terms used to describe the relationships between crops, plant pathogens and plant pests more broadly were reviewed by Bos and Parlevliet (1995) to establish a level of consensus among crop protection researchers and practitioners. They also present the terms tolerance and sensitivity as inversely related characteristics denoted by the same mechanism, but point out, as with resistance and susceptibility, that underlying mechanisms may operate independently and simultaneously in plants. For that reason, they introduce the term vulnerability (high or low) to integrate the effects on crop plants. The authors critiqued the definitions of Schafer (1971) in that only the disease is tolerated, not the pathogen. They also critiqued Cooper and Jones (1983) in that their definitions only covered tolerance to attack, where the term attack derives from its everyday use and can be seen in relation to pathogens seen as harmful or hostile organisms. In the Cooper and Jones (1983) review, pathogen attack is used to cover all infection events from pathogen multiplication, colonisation, and internal spread. Hence, only the pathogen is tolerated.

The uses of disease tolerance as introduced by Schafer (1971) and attack tolerance as introduced by Cooper and Jones (1983) were refined by Clarke (1986) who used the terms "tolerance of the pathogen," "tolerance of disease," and "overall tolerance." Tolerance of the parasite was defined as "the ability of a plant to endure the effects of levels of parasitic infection which, if they

occurred at equivalent levels in other plants of the same or of similar species, would cause greater damage or disease." Tolerance of disease was defined as "the ability of a plant to endure the effects of levels of disease, which, if they developed to equivalent levels in other plants of the same or similar species, would cause greater impairment of growth or yield." Finally, overall tolerance was defined as "the ability of a plant to endure the effects of levels of parasitic infection and disease, which, if they occurred at equivalent levels in other plants of the same or similar species would cause greater impairment of growth or yield". As will be discussed later the use of and emphasis placed on the term "equivalent" is of critical importance but has been much ignored in recent literature. The review then outlines methods (at that time) of measuring parasite biomass, the amount of disease, the degree to which growth or yield is depressed, the importance of equivalence, and prospects for measuring the different forms of tolerance. Methods may have changed over the last three decades, but these principles remain valid. A series of case studies at that time examined the evidence for tolerance to viruses, fungi, and bacteria. For the first time, tolerance as a host survival strategy and its evolution in wild hosts was examined. Finally, the physiological basis of both forms of tolerance was reviewed and examples of practical applications discussed.

2.3 | A modern consensus?

A comprehensive and unifying review of tolerance in plants was made by Pagán and García-Arenal (2018, 2020). Tolerance was defined as the ability of the host to reduce the effect of infection on its fitness regardless of the level of pathogen multiplication, whereas resistance is the ability to reduce pathogen multiplication (Pagán & García-Arenal, 2018). In a review aimed at summarising experimental and theoretical studies on plant tolerance to pathogens, the authors concluded the following:

1. In plant–pathogen systems, resistance and tolerance generally coexist,
2. Evidence of tolerance polymorphisms is abundant,
3. Tolerance is an efficient strategy to reduce the damage, and
4. There is no evidence that tolerance results in increased pathogen multiplication.

It is important to note that how plant fitness is assessed can depend on the context and the relative importance of fecundity and mortality in the plant-pathogen interaction: hence, the terms mortality tolerance and fecundity tolerance were used. It is necessary to distinguish between reproductive fitness (ruderal characteristics) or vegetative fitness expressed in differences in plant growth rate and biomass which then leads to competitive advantage. There is also some debate on the relevance of plant fitness for crop plants where individual plant fitness is sometimes mistakenly equated with crop improvement (Abbai et al., 2020).

The co-evolutionary aspects of tolerance were stressed in Pagán and García-Arenal (2018) and the need to consider both plant and pathogen fitness. A distinction is made between point and range tolerance as these may lead to different interpretations of the host response shown schematically in Figure 1. Host tolerance is considered as a genotype-specific trait assessed as the slope of host fitness against pathogen burden rather than an individual plant-based trait, as also suggested for animal diseases (Kause & Ødegård, 2012). The possibility of an increase in host fitness as virus load increases is also shown. A comprehensive review was made directed to the broader plant pathology community (Pagán & García-Arenal, 2020) that attempted to not only reconcile the differing concepts but also point out the ambiguities and contradictions that remain and the difficulties in quantifying tolerance. They return to the earlier discussions and stress the importance of "endurance" (Clarke, 1986; Schafer, 1971) as a means of clarifying usage of the term tolerance.

3 | TOLERANCE AND RESISTANCE

It is insightful to contrast how resistance and tolerance are referred to. It may simply be a linguistic artefact but commonly the usage "resistance **to** a plant pathogen" versus "tolerance **of** a plant pathogen" is found, reflecting perhaps unappreciated differences in the plant response in which resistance acts directly on the pathogen and tolerance on the effects of the pathogen (Jeger, 2020; Jeger et al., 2006): to return to the earlier point, there is endurance **of** disease. Possibly due the ambiguity in the term, studies related to tolerance have not always used the term to describe the host response. From studies with the pathogenic fungus *Zymoseptoria tritici*, Bancal et al. (2016) concluded that disease development and apical senescence behaved independently as disease was never shown to accelerate or anticipate apical senescence. In a review of plant health concepts, resilience was termed the ability of a plant to withstand stress caused by pathogens or abiotic disorders, with or without human interventions (Doring et al., 2012). Is such an ability a surrogate measure of tolerance?

Tolerance ("true tolerance") was defined by Politowski and Browning (1978) for cases in which a cultivar has a

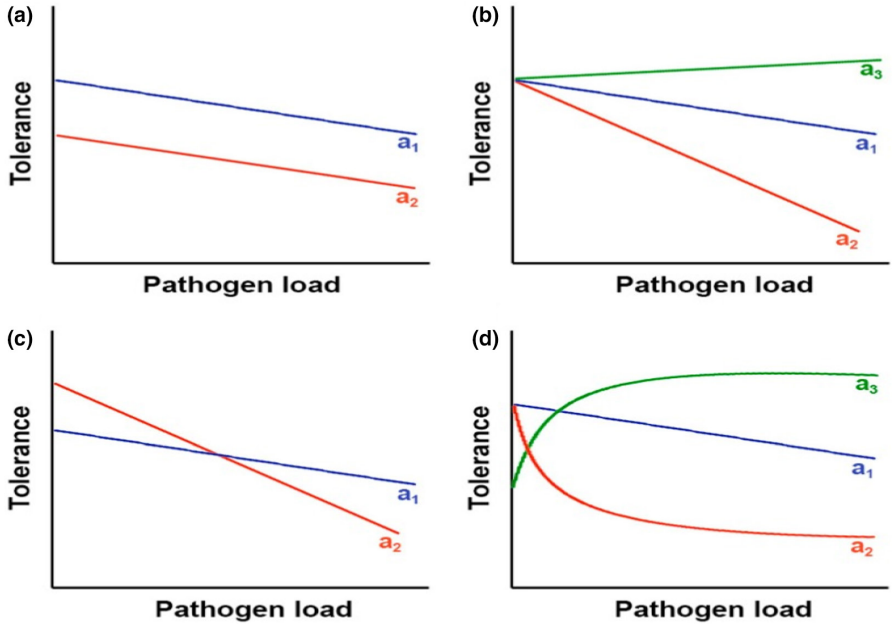

FIGURE 1 Schematic illustrating point and range tolerance (Pagán & García-Arenal 2018, figure 1, re-used under creative common CC BY license, with legend modified from the original). (a) Host genotype a1 has higher fitness than genotype a2 when uninfected and at every pathogen load, but range tolerance is the same in both genotypes. Point tolerance will always indicate higher tolerance of genotype a1; (b) host genotypes a1 and a2 have the same fitness when uninfected, but range tolerance is higher in a1 than in a2. Genotype a3 overcompensates detrimental effects of infection at every pathogen load; (c) host genotype a1 has lower fitness than genotype a2 when uninfected, but range tolerance is higher for genotype a1 than for a2; (d) both genotypes have the same fitness when uninfected. Range tolerance is linear for genotype a1 but not for genotype a2. Genotype a2 has lower range tolerance than a1 in the early non-linear phase but the response levels off as virus load increases. Genotype a3 overcompensates the detrimental effect of pathogen infection up to a maximum.

susceptible infection type and supports the same amount of pathogen as another cultivar but has significantly better yield and quality, or the same yield and quality as another cultivar but supports significantly more of the pathogen. Experimental work was done with the rust *Puccinia coronata* and oat cultivars in a study comparing tolerance with different forms of host resistance. This definition stresses the importance of equivalence whether attached to the pathogen or to yield and that the term is essentially relative rather than absolute. A distinction was made between tolerance at the individual plant level and reduced incidence at the field level termed tolremicity and illustrated in field trials for maize streak virus (MSV) disease (Bosque-Pérez et al., 1998) aimed at characterising field resistance, seen as a combination of individual plant tolerance and a reduced population incidence.

In considering the genetic improvement of new and orphan crops, Dawson et al. (2019) collated the views of 53 African plant breeders across 30 specific plants of nutritional significance and identified priorities from a range of genetic targets. Pest and disease tolerance and host resistance were identified as the priority genetic traits followed by yield. Natural tolerance to MSV and its monogenetic control has been described although emphasis has been placed on concentrating resistance genes in maize genotypes (Shepherd et al., 2010). In some cases where sources of resistance are not available, such as in onion to iris yellow spot disease, field tolerance can play an important role and may be interpreted as a response to plant stress from the virus or the thrips vector (Bag et al., 2015).

3.1 | Assessment of tolerance

Tolerance as a disease management strategy has been claimed to be as widespread as host resistance although problems remain not only in the definition of tolerance but also how it can be assessed (Pagán & García-Arenal, 2020). For some workers, especially those concerned with crops, it refers to limited symptom development or reduction in plant vigour or yield in a cultivar despite a normal virus accumulation that would be expected in a susceptible cultivar. For other workers, more concerned with the ecological and evolutionary aspects of plant–virus interactions, tolerance would be measured as the limited reduction in plant fitness (fecundity, reproduction period). In a resistant (not immune) variety, there would be limited virus accumulation and symptom development, although there may be a penalty in terms of reduced vigour and yield in the absence of disease compared with a susceptible

variety. Tolerance (reduced symptoms and virus levels throughout a plant's life) differs from "non-recovery accommodation" in that in the latter there is no recovery from symptoms (Bengyella et al., 2015), but such a finding begs the question does tolerance necessarily involve recovery?

Paudel and Sanfaçon (2018) proposed that tolerance of plant viruses can be manifested as a balance between plant defence responses and the counter responses of the virus. This concept has been criticised as failing to distinguish between tolerance and partial resistance seen as somewhat intermediate between immunity and full susceptibility (Pagán & García-Arenal, 2020). This is perhaps not so much a criticism of the concept, but a reflection that different views and interpretations of tolerance continue. Infection rates determined by vector inoculation and agroinfection and PCR showed lower virus accumulation in infected cultivars compared with susceptible cultivars without symptoms of wheat dwarf virus (Benkovics et al., 2010) but is this simply partial resistance rather than tolerance in which virus accumulation was not reduced but dwarfism was reduced? Similar comments apply to the molecular studies on the plant response to infection by tomato yellow leaf curl New Delhi virus, in which graded classifications from tolerance to full susceptibility were made, essentially characterising partial resistance (Sahu et al., 2010). A naturally tolerant tomato cultivar was shown to have "delayed lower infectivity, late symptom appearance, reduced viral loads, and less symptom severity" than a susceptible cultivar when challenged with tomato leaf curl New Delhi virus, with both viral DNA methylation and siRNA-mediated RNA degradation underlying this expression of tolerance (Sahu et al., 2014). Clearly, this analysis is confounding resistance and tolerance and indeed no attempt is made to draw a distinction between the two traits. By contrast resistance and tolerance traits were clearly differentiated for tomato brown rugose fruit virus (Zinger et al., 2021), with the tomato genome loci controlling these traits identified and mapped. Contrary to expectation, control of the tolerance trait was by a single recessive gene, whereas at least two additional genes were required to confer resistance.

Very few studies have attempted to quantify and model the level of tolerance of plant viruses. Rubio et al. (2003) proposed three formulae to calculate a resistance index, a tolerance index, and a combined resistance-tolerance index that was applied to tomato yellow leaf curl disease. The indices were based on number of infected plants and virus titres (resistance), number of infected plants and symptom severity (tolerance), and a combination of these quantities (resistance-tolerance). In each case the indices scale as 0–1. Soler et al. (2015) proposed indices based on Kaplan–Meier survival times without infection (a measure of resistance) or the presence of severe symptoms (a measure of tolerance) for tomato spotted wilt virus in a new accession of pepper (from *Capsicum baccatum*). The absence of severe symptoms in the new accession compared with the susceptible check was maintained when plants were inoculated with a resistance-breaking strain of the virus (Figure 2). Bayesian survival analysis was used by the same group to evaluate resistance (time from virus inoculation to virus detection in plants) and tolerance (time from virus inoculation to appearance of severe symptoms) in a new plant genotype compared with a susceptible and resistant genotype (Lázaro et al., 2017). Two virus biotypes were used in the studies but no information on plants or virus was provided in the publication, a technical Proceedings on Bayesian statistics. It is assumed that the data analysed are for the same pepper–tomato yellow leaf curl disease (TYLCV) system (Soler et al., 2015) as the results of the analysis showed the same results as in the earlier publication.

Despite the ambiguity and controversies surrounding the use of the term tolerance in plant pathology, paradoxically it has been claimed that the distinction made from host resistance could be followed in animal science (Råberg et al., 2009), in which point tolerance refers to fitness costs for a given pathogen burden and range tolerance refers to the slope of the linear regression between host fitness and pathogen fitness. Evaluation of tolerance in perennial host plants, such as fruit trees, presents a further set of methodological problems, not least the need for longer term evaluation where recovery from symptoms occur, as opposed to non-recovery responses referred to earlier (Bengyella et al., 2015). Genetic dissection of Sharka disease tolerance in peach was made based on evaluation of peach germplasm collections, with tolerance defined as virus replication and spread through graft-infected plants but with either none or only mild sporadic symptoms (Cirilli et al., 2017). The aim using a genome-wide association approach was to identify genetic loci controlling quantitative expression of tolerance and to develop markers that could be used in breeding programs.

3.2 | Durability of tolerance and resistance

Fraile and García-Arenal (2010) discussed resistance and tolerance in relation to the co-evolution of plants and viruses. They considered that the lack of studies of wild plants in natural ecosystems in response to virus infection was a major limitation with little known of the effect of quantitative resistance or tolerance on plant fitness, a necessary first step determining the occurrence of co-evolution. Considering co-evolutionary aspects raises

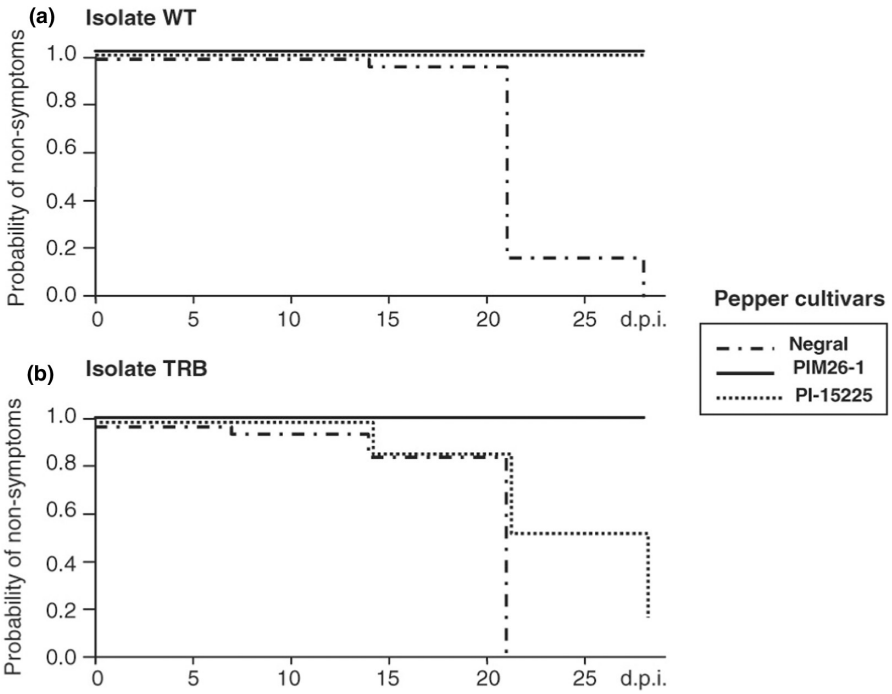

FIGURE 2 Kaplan–Meier survival curves showing the probability of no presence of severe symptoms over time for two TSWV isolates: Da1NL2 (biotype wild type, WT) and Alm1 (biotype Tsw resistance-breaking, TRB) and three pepper accessions: Negral (susceptible), PIM26-1 and PI-159236 (with the resistance gene Tsw) (Soler et al., 2015, Figure 3, re-used with permission from John Wiley and Sons, with legend modified from the original). Thirty replicates were used per isolate and pepper accession.

question concerning both the durability of resistance and tolerance, and the fitness costs and trade-offs involved in evolutionary trajectories (Lecoq et al., 2004).

Montarry et al. (2012) in a study of polygenic quantitative resistance to potato virus Y in pepper found that adaptation to quantitative resistance could lead to resistance breakdown, associated with a fitness cost of disease on a susceptible cultivar, but that adaptation was not correlated with the extent of damage caused by the virus. One explanation could be the high tolerance level found in the susceptible cultivar. The definition made of tolerance is important as it will determine whether the concept of tolerance breakdown can occur. A cultivar of squash considered tolerant to zucchini yellow mosaic virus showed symptoms when infected with several virus isolates suggesting the tolerance was overcome (Romay et al., 2014). The importance of estimating the specificity and durability of resistance and tolerance to viruses was demonstrated in melon for cucumber vein yellowing virus, where few resistance sources are available (Desbiez et al., 2022). Resistance was found to be isolate specific with severe symptoms caused by one isolate that differed in only one amino-acid change from the parental strain. Tolerance presented a much broader range of mild symptoms despite virus accumulation in inoculated plants, that is, illustrating tolerance of the virus.

3.3 | Tolerance trade-offs and fitness costs

In a study comparing the costs and benefits of resistance to and tolerance of plant disease (Simms & Triplett, 1994), looked at fitness costs in *Ipomoea purpurea* and the fungal pathogen *Colletotrichum dermatium* using diallel crosses from weed seedlings to produce full-sib and half-sib families and inoculated or remained healthy. Fitness was assessed as the total number of fruits flowers and flower buds, an estimate of reproduction potential including both maternal and paternal components. Tolerance was defined as the slope of a regression of fitness against pathogen damage, additionally as the difference in reproductive performance between infected and healthy plants. Tolerance defined in either way gave evidence for fitness costs and a trade-off between tolerance and resistance. They concluded that selection cannot act on resistance without also influencing tolerance, and vice-versa.

Mikaberidze & McDonald (2020) contrasted tolerance with resistance, in which "tolerance alleviates the reduction in host fitness due to infection without reducing a pathogen's growth," whereas "resistance reduces pathogen growth." In plots of host fitness against the pathogen population, or burden, two cultivars may have the same average pathogen burden, but one is defined as more tolerant if the slope of host fitness against pathogen burden is steeper. A major study was undertaken in which some 11,000 leaves infected with *Z. tritici* across 335 wheat cultivars were examined for green leaf area (assumed to be a measure of host fitness) and number of fruiting bodies (assumed to be a measure of pathogen growth) with some 2 million pycnidia counted. A negative relationship was found between tolerance and resistance suggesting a trade-off between the two traits, interpreted as due to resource limitation rather than metabolic constraints.

The genetic variation in tolerance of and resistance to cucumber mosaic virus (CMV) in the herbaceous (and

invasive) plant *Mimulus guttatus* was studied using a diallel crossing design in greenhouse-grown potted plants (Carr et al., 2006). The questions asked were: what are the levels of genetic and environmental variation in this system, is there evidence for a cost of resistance or tolerance, and is there evidence for a trade-off between the two traits? With respect to the last question, the expectation was a negative genetic correlation, although as pointed out tolerance (defined as the difference in flower production and aboveground biomass between infected and healthy plants) and resistance (virus accumulation in the leaf tissues) would often be confounded (resistant plants with low-level infections would exhibit "apparent high tolerance," whereas less resistant plants with higher levels of infection would exhibit "apparent low tolerance"). Given this proviso, phenotypic variation was found for both tolerance and resistance but low narrow-sense heritability, no evidence for a cost of either tolerance or resistance, and no evidence for a trade-off between the two traits. They concluded that selection would favour the same *M. guttatus* genotypes irrespective of whether these were infected or healthy.

Whether there are trade-offs in tolerances to different viruses was studied recently in *Arabidopsis thaliana* genotypes challenged with either CMV or turnip mosaic virus (TuMV) (Montes & Pagán, 2019). It was found that tolerance to CMV was associated with resource allocation from growth to reproduction, whereas for TuMV it was associated with the time to and length of the reproductive period. There was a genotype-dependent trade-off in tolerance between the two viruses. This finding carries implications for disease management based on tolerance, in particular reproductive stage tolerance, when more than one virus is present in a crop. Mixed infection with different viruses may also affect the expression on tolerance. Mixed infection of cucumber (*Cucumis sativus*) with zucchini yellow mosaic virus (ZYMV) and CMV showed a synergistic effect increasing the level of damage (Möller et al., 2006). None of the cucumber cultivars tested were resistant to ZYMV, although some were tolerant of CMV in single infection.

Whether there are fitness costs associated with tolerance may depend on strains within the virus population. Increased aggressiveness, defined as the ability in induce severe symptoms, of ZYMV was observed on hybrid cultivars of zucchini squash (*Cucurbita pepo*) (Desbiez et al., 2003), previously considered to be tolerant rather than resistant as systemic virus multiplication occurred. A point mutation in the viral P3 protein (associated with the viral replication complex) was sufficient to induce the increase in aggressiveness and apparent breakdown of tolerance. In mixed infections of the more aggressive mutant strain had greater fitness than the wild-type ZYMV. However, counter-selection against the mutant in fully susceptible cultivars of squash (and/or melon) might led to a degree of durability in tolerance.

According to Badet et al. (2019) from an evolutionary perspective, high levels of tolerance may release selection at resistance genes and that the boundary between tolerance and quantitative disease resistance may be unclear with some overlap with epistasis, where the expression of one gene is affected by the expression of one or more independently inherited genes. The authors found evidence that loci controlling plant morphology and development in *A. thaliana* were associated with quantitative disease resistance to the necrotrophic fungus *Sclerotinia sclerotiorum*. AUGUSTIFOLIA (AN) is a C-terminal binding protein found in animals and plants. In plants it is involved in the morphogenetic development of leaves and floral organs. Collectively, AN is involved in plant development and disease tolerance (Xie et al., 2020). In studies with *A. thaliana*, a trade-off in defences against (hemi)biotrophic and necrotrophic pathogens was demonstrated.

3.4 | Plant reproductive stage stress tolerance

Recent work has placed more emphasis on fecundity or reproductive stage stress tolerance to a range of biotic and abiotic stressors. There is an increased recognition of the importance of seed transmission in the epidemiology of many plant viruses (Pagán, 2022) (Figure 3). Studies were carried out with *A. thaliana* challenged with either CMV or TuMV (Montes & Pagan, 2019) to identify effects of light intensity on virus multiplication, tolerance, and seed transmission. High light intensity increased TuMV multiplication and tolerance and was associated with more efficient seed transmission. By contrast, high light intensity reduced CMV multiplication and tolerance and had no effect on seed transmission. Tolerance of plant viruses may be expressed as a switch in resource allocation from vegetative growth to reproduction or in the length of the pre-reproductive period, depending on the level of virulence in the virus (Shukla et al., 2018). With *A. thaliana* and CMV, a relatively low virulence virus, tolerance was associated with resource re-allocation; however, with other more virulent viruses on this host the length of the pre-reproductive period was extended.

The emphasis on reproductive stage tolerance offers many opportunities to link the effects of biotic and abiotic stressors on plant genetics, physiology, and disease ecology. This will require a whole life history approach. For example, with annual plants and indeterminate flowering: seed germination and seedling emergence occur on shorter time scales than vegetative plant growth;

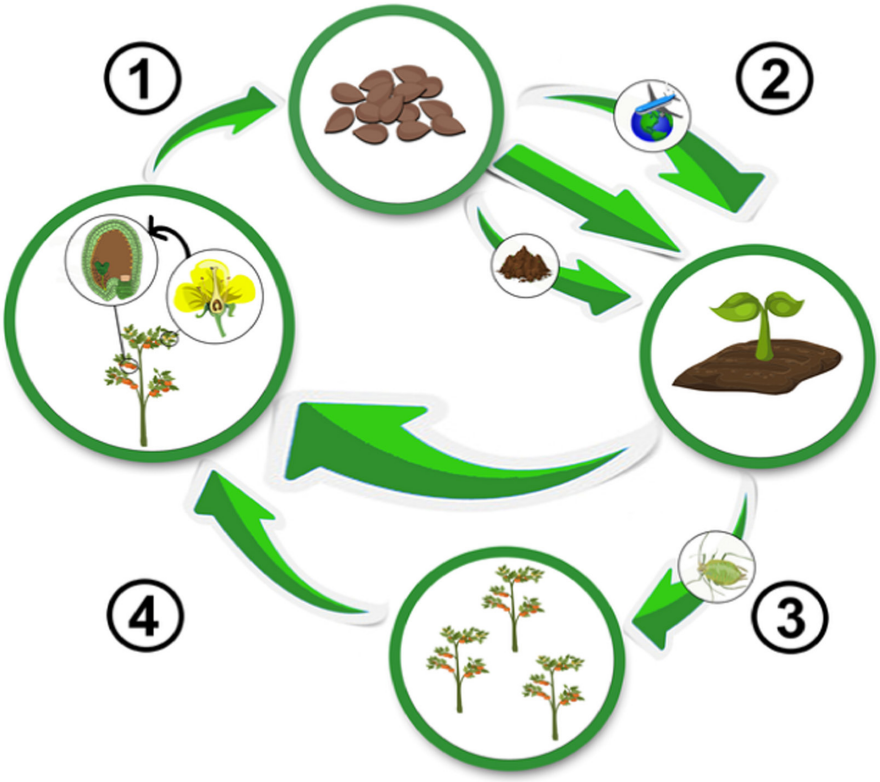

FIGURE 3 Virus seed transmission cycle (Pagan, 2022; Figure 1, re-used under creative commons attribution licence, with legend modified from the original). (1) plant viruses reach seeds either by direct invasion of the embryo from the parental plant and/or indirectly by infecting pollen grains or ovules. (2) infected seeds may directly germinate; remain for long periods of time in the soil; or be dispersed to long distances. In any of these scenarios, infected seed will produce infected seedlings after germination. (3) infected seedlings, eventually adult plants, from infected seeds will be sources of primary inoculum allowing onward transmission through vectors. (4) the cycle can be closed when viruses from infected plants reach seeds leading to the second round of seed transmission, or plants infected by vectors can produce infected seeds.

flowering may occur at any time during the growth period, which also corresponds to the pollination period; at the end of the growth and pollination period, seeds drop, and eventually the plant dies; and only seeds that survive the overwintering period start a new cycle if there is no seedbank. The challenge in is then to disentangle the interactions with plant virus epidemiology.

A ruderal species is a plant species that is first to colonise land that is repeatedly disturbed. According to Grimes's CSR theory of ecological strategies (competitors, stress-tolerance, ruderals) (Grime, 1977), ruderal species invest in rapid reproduction and propagule dispersal. A further element of the theory is that plants cannot optimise tolerance to both pathogen infection and drought. In annual plants, reduced growth and delayed reproduction can be features of exposure to water stress; however, with severe water stress, an increase in growth rate and earlier reproduction can result as an escape strategy. Bergès et al. (2020) tested the hypothesis that ruderality is positively related to virus infection irrespective of water availability, using the model system *A. thaliana*. They found that tolerance of cauliflower mosaic virus infection (measured in terms of vegetative performance) among *A. thaliana* accessions was positively associated with early flowering, and further that plant survival of infected plants increased with water deficits.

Virus infection has been shown to improve drought tolerance. In a study of pollinator preference of bumblebees for healthy susceptible or infected plants (Groen et al., 2016), it was found that attraction in tomato infected with CMV is controlled by the CMV 2b gene, the same gene that controls drought resistance in infected *Arabidopsis*. How the preferential attraction of pollinators to infected plants may be affected by reproductive tolerance to CMV infection was not studied in detail. The authors suggested that increases in reproductive success of infected plants through pollinator attraction would outweigh any selection for resistance, thus favouring the virus and the host, and perhaps the development of tolerance in the host population in which there is no decrease in reproductive fitness with infection.

Viruses have been used to induce flowering as a means of accelerating plant breeding programmes, especially for those plant species which show delayed

or recalcitrant flowering (McGarry et al., 2017). In essence, viruses can be used as vectors for the FT ortholog-enabling systemic movement of the gene product florigen to apical meristems. Such an approach has regulatory issues to be resolved. A specific example of this approach is given for the breeding of grapevine using apple latent spherical virus (ALSV) as the vector (Maeda et al., 2020), where the virus is asymptomatic. No seed transmission occurred, and virus was successfully eliminated from infected grapevine through heat treatment to allow ALSV-free shoots to be produced. Seed transmission of viruses in plant breeding, such as banana bract mosaic virus in *Musa* synthetic diploids (Selvarajan et al., 2020), would be a serious issue in banana breeding if tolerance was present in breeding lines. The "aesthetic" value of some ornamental plants can be enhanced through virus symptoms on flowers (Valverde et al., 2012) and in these cases the reduced symptoms aspects of tolerance would not be valued. Floral traits, pollen associated viruses, and plant pollinator interactions have recently been reviewed (Fetters et al., 2022), but the nature of these association whether of a cryptic or tolerant nature have been little explored.

4 | CASE STUDIES ON TOLERANCE OF PLANT VIRUSES

Despite the extensive work done on plant resistance to viruses (see reviews by e.g., Calil & Fontes, 2017; Mandadi & Scholthof, 2013; Wang, 2015), there is little information on the molecular basis of tolerance of plant viruses. An exception is the work of Amoroso et al., 2022 who used transcriptomic and genomic analyses to dissect the molecular and genetic processes involved in tolerance of Zucchini yellow mosaic virus in squash.

Many studies have investigated tolerance using the model plant *A. thaliana* and associated viruses in laboratory/microcosm studies. In this system, it was found that tolerance mechanisms may lead to a lack of association between virulence (deleterious effects of the virus on the host) and virus multiplication (Pagán et al., 2007). Host density and virus infection interact to either increase or decrease the competitive ability of the host (Pagán et al., 2009). In this study, tolerance to the direct costs of infection by the virus arises from a switch from growth to reproduction, whereas tolerance to the indirect costs of infection (from competitive ability) arises from a higher investment in growth. Tolerance to abiotic stress and infection (CMV) in *A. thaliana* was achieved through resource allocation from growth to reproduction (Hily et al., 2016). Here tolerance is defined as decreasing virulence irrespective of the amount of virus multiplication; also, as found in the same system with Montes et al. (2019). Tolerance to TuMV traded off with tolerance to CMV (Montes et al., 2020). A high proportion of tolerant genotypes in a heterogeneous population was found to promote virus multiplication, reduce the effect of mortality from virus infection, but not plant fecundity (Montes et al., 2021).

For crops a considerable effort has been made in breeding for plant tolerance, notably in cereals and barley yellow dwarf viruses (BYDVs) by identifying quantitative trait loci for tolerance (Ayala et al., 2000, 2002, del Blanco et al., 2015, Hu et al., 2019, Kosová et al., 2008, Riedel et al., 2011, Scheurer et al., 2001, Scholz et al., 2009). Almost invariably, tolerance is confounded with field resistance with no distinction made between resistance and tolerance in phenotyping/genotyping; also, when considering both the virus and vector in evaluations (Silva et al., 2022). In many crop-breeding programs (Table 1), phenotyping tends to be done by characterising lines as susceptible, tolerant, or resistant by reference to check cultivars, but without considering the original basis for these categories being made or for the environments in which the trials are made (e.g., Camara et al., 2013; Quesenberry et al., 2010; SumanSahu Das & Dwivedi, 2018; Wang et al., 2017). For viruses of other crops, a range of breeding trials and genetic studies on plant tolerance has been done (Table 1).

As with plant breeding programs, much field-based evaluation of tolerance has been done with BYDVs (Hoffman & Kolb, 1998; Jarošová et al., 2013; Niks et al., 2004; Weisz et al., 2005), and usually emphasise the use of mapping populations, yield-related aspects of tolerance, and how this varies in different environments. A tolerant variety is often considered as expressing field resistance compared with one expressing susceptibility to the viruses. Very rarely are yield estimates made in conjunction with epidemiological assessments of visual symptoms or virus load as disease develops in the field. With other crop/virus systems shown in Table 2, tolerance was not differentiated from quantitative host resistance (e.g., Eid et al., 2006).

By comparison with work on tolerance of virus infection (and disease), less has been done on tolerance of vector feeding and damage. Tolerance of the virus in vectors enables transmission success where the vector-virus interaction is not simply transient but persistent within the vector. This is assured by the balance between apoptosis and autophagy as found for the whitefly (*Bemisia tabaci* MED), the vector of TYLCV (Wang, Guo, Ge, & Sun, 2022; Wang, Guo, Zhu-Salzman, et al., 2022). Many studies have used tolerance to refer to the insect, for example, thermotolerance (Aregbesola

TABLE 1 Main findings from representative breeding programs and genetic studies on tolerance across a wide range of plant viruses. The studies are ordered alphabetically by first author, rather than by crop or plant species.

Crop/plant species	Virus	Main finding/comment	Source
Squash/*Cucurbita pepo*	Zucchini yellow mosaic virus	Transcriptome analysis of a tolerant cultivar derived from introgressed genomic regions from *C. moschata* showed a reduction in virus titre, increased photosynthetic and photorespiratory activity, and alleviated symptoms	Amoroso et al. (2022)
Black gram/*Vigna mungo*	Yellow mosaic virus	YMV-tolerant lines were crossed with susceptible cultivars and inoculated with infective whiteflies. Segregation analysis showed a monogenic recessive form of control. A DNA marker was found to be linked with the YMV-tolerant phenotype	Basek et al. (2004)
Tomato/*Solanum lycopersicum*	Tomato yellow leaf curl virus	A breeding program was undertaken in Senegal to identify resistance in tomato varieties by reference to susceptible, tolerant, and resistant cultivars. More tolerant than resistant varieties were identified, but yield was correlated with resistance rated at the time of flowering.	Camara et al. (2013
Onion/*Allium cepa* and *A. cepa* var *cepa*	Iris yellow spot virus	Tolerance to thrips feeding and thrips preferences, rather than host resistance to the virus, together with a wide tolerance to stress, form the background to tolerance of IYSV expressed as less severe symptoms	Cramer et al. (2014)
Rhizoma perennial peanut/*Arachis glabrata*	Peanut stunt virus	Two new released cultivars showed improved 'field' tolerance to PSV compared with a commercial type-cultivar, with equivalent dry matter yield and weed competitiveness	Quesenberry et al. (2010)
Cassava/*Manihot esculenta*	South African cassava mosaic virus	Tolerance of SACMV in cassava landraces was characterised by a recovery from virus infection, with susceptibility characterised by cultivars continuing to be susceptible throughout the infection period. Proteome analysis suggested that chloroplast and ribosomal proteins played a role in the tolerance expressed	Ramulifho and Rey (2022
Potato/*Solanum tuberosum*	Potato virus Y	PYV achieved high levels of systemic infection in Russet Burbank but without phenotypic effects in plants grown from tissue culture. MicroRNAs were suggested to facilitate tolerance with a possible link to the development of mutualism in plants	Ross et al. (2022)
Potato/*Solanum tuberosum*	Potato mop top virus	An early maturing potato variety was found to be 'insensitive' (considered as tolerant with reduced tuber symptoms) to the virus compared to the 'sensitivity' of Russet Burbank, but with different levels of susceptibility/resistance to other viruses (and pathogens).	Stark et al. (2018)
Okra/*Abelmoschus esculentus*	Yellow vein mosaic virus	New methods were proposed to extract genomic DNA, overcoming previous difficulties due to the high levels of polysaccharides in okra. A molecular (RAPD) marker was developed for identifying tolerance, different to markers	SumanSahu Das and Dwivedi (2018)
Rice/*Oryza sativa*	Southern rice black-streaked dwarf virus and rice ragged stunt virus	Proteomic studies were made to compare the different mechanisms of tolerance and sensitivity in rice cultivars to SRBSDV, considered as aspects of resistance and susceptibility, using a range of agronomic, disease, virus load, and vector population parameters.	Wang et al. (2017)

TABLE 2 Main findings from representative field-based evaluation of tolerance across a wide range of plant viruses. The studies are ordered alphabetically by first author, rather than by crop or plant species.

Crop/plant species	Virus	Main finding/comment	Source
Highbush blueberry/ *Vaccinium corymbosum*	Blueberry scorch virus	A multi-year study on transmission, spread, and yield loss was made with >50 varieties. Half were found to infected but symptomless; six tolerant varieties were identified, which showed no significant yield loss despite being infected with the virus.	Bristow et al. (2000)
Canola/*Brassica napus*	Turnip yellows virus	A series of glasshouse experiments investigated the impact of TYV on seed yield in an open-pollinated and a hybrid cultivar. No reductions in seed yield were observed in the hybrid cultivar inoculated at the start of stem elongation, indication tolerance to infection at this growth stage.	Congdon et al. (2020)
Banana and plantain/ *Musa* spp hybrids	Banana streak virus	Plantain and banana micropropagated hybrids were evaluated in the field for natural symptom incidence, virus indexing and relative antigen concentration. Some of the hybrids tested were found to be 'field tolerant' but such a classification may only apply in warmer environments.	Dahal et al. (2000)
Cucumber/*Cucumis sativa*	Cucurbit yellow stunting disorder virus	Cucumber accessions were evaluated for disease reaction when inoculated with CYSDV under high inoculum pressure. Although no accessions were immune, leaf samples were taken from plants previously designated as tolerant showed delayed and milder symptoms than those designated as susceptible. Virus titres in the tolerant accessions were significantly lower than in the susceptible accessions.	Eid et al. (2006)
Tomato hybrids/*Solanum lycopersicum* x *Solanum peruvianum*	Tomato chlorosis virus	Field trials evaluated the response of tomato to ToCV, with plant development and fruit yield compared between healthy and infected plants. Only one hybrid line from 56 genotypes was highly resistant. Tolerance was found to be highly variable with reductions of ~3–72% in development and ~0.2–52% in yield.	Manzilla-Córdova et al. (2018)
Hot pepper/Capsicum annuum var. *annuum*	Potato virus Y and Ethiopian pepper mottle virus complex	Variability in the 'genetic' tolerance of the two viruses was found in pepper genotypes. The tolerance shown by infected by symptomless genotypes could be used in resistance breeding and combining early aphid exclusion with tolerant cultivars could minimise fruit losses.	Marame et al. (2010)
Winter wheat/*Triticum aestivum*	Wheat streak mosaic virus	The susceptibility and tolerance of wheat varieties to WSMV were studied in the Great Plains area of the US. All varieties were susceptible but variations in tolerance (yield losses following virus infection) were found, with some evidence for a climatic effect.	Miller et al. (2014)
Groundnut/*Arachis hypogaea*	Tomato spotted wilt virus	This study proposed a physiologically based mechanism for tolerance of TSWV, whereby near-normal photosynthetic activity was maintained in symptomless tissue even in the presence of virus infection.	Rowland et al. (2005)
Groundnut/*Arachis hypogaea*	Tomato spotted wilt virus	The observed 'field' resistance of some groundnut genotypes (widespread but limited incidence of TSWV disease) was attributed to tolerance. There were minor thrips fitness effects on susceptible and resistant genotypes.	Shrestha et al. (2013)
Soybean/*Glycine max*	Bean pod mottle virus and tobacco ringspot virus	More than 300 cultivars were inoculated and screened for resistance or tolerance in the greenhouse. For BPMV, a range of tolerance was found based on lesser reductions in height and biomass of infected plants. For TRSV, all cultivars showed early symptoms but some 56 recovered from symptoms while systemically infected and showed tolerance at later growth stages.	Shakiba et al. (2012)
Tomato/*Solanum lycopersicum*	Tomato yellow leaf curl virus	In a year when virus pressure was high and chemical control of whiteflies ineffective, yield in susceptible cultivars was extremely low but was less affected in tolerant varieties. Egg and nymph whitefly populations were lower on tolerant varieties.	Smith et al. (2019)

et al., 2019), starvation tolerance (Xu et al., 2016), or insecticide tolerance and potential fitness costs (Skaljac et al., 2018), with any effects on virus transmission considered only implicitly. A recent study has shown how salinity stress in the plant can affect both aphid life history characteristics and virus transmission (Parizipour et al., 2021). Survival rate and longevity of viruliferous *Rhopalosiphum padi* on saline stressed wheat were significantly reduced. This is an example how an environmental stress acting on the plant can have a large effect on insect vector and virus transmission. And yet in terms of host tolerance to vector feeding and reproduction (in the pathogen tolerance sense) there may also be clear implications for virus transmission. Cultivars of winter wheat have been identified that tolerate the effects of feeding damage by the aphid vector *R. padi* and sustain significantly greater aboveground biomass (Girvin et al., 2017), which must affect the transmission of the RPV strain of BYDV, although this aspect was not covered in the study. Compensatory physiological processes were found to be involved in a plants ability to withstand large insect hemipteran populations without, importantly, impairing the insect's reproduction and behavior (Koch et al., 2016). Hemipteran insects include aphids and whiteflies, the most important virus vectors, and because there appears to be no effect of tolerance on these insects there is no reason to suppose that tolerance to vectors will lead to reduced virus transmission. Plausible physiological mechanisms were proposed allowing a conceptual means of differentiating resistance, induced tolerance, constitutive tolerance, and susceptibility as host responses to feeding damage.

A largely unanswered question is can virus infection lead to tolerance to the direct pest effects of insect vectors (Riedell, 1999)? Induced salicylic acid and jasmonate reponses in plants are affected by CO_2 in different interactions which may affect the plant response to both virus infection and vector feeding (Bazinet et al., 2022).

5 | OTHER PATHOGEN TAXA

5.1 | Fungal pathogens

Although the main emphasis of this review has been on plant viruses, earlier work on other pathogen taxa has been cited where appropriate (Politowski & Browning, 1978, Simms & Triplett, 1994) especially for fungal pathogens. Boundaries between quantitative disease resistance and tolerance are often unclear (Badet et al., 2019). Based on work on *S. sclerotiorum* quantitative resistance in *A. thaliana*, disease tolerance reduces the impact of pathogen infection on plant fitness and by doing so may reduce selection on resistance genes. Effectiveness against a broad range of pathogens and an epistatic interaction between tolerance and resistance may be expected.

Much work has been done with *Z. tritici* causing septoria leaf blotch of wheat. The work of Mikaberidze and McDonald (2020) on the relationship between tolerance and resistance, in which a potential trade-off between these defence mechanisms was identified, was discussed earlier. Traits conferring tolerance of *Septoria tritici* blotch were clearly defined in terms of source-sink relationships, green leaf area duration, and grain weight (Bancal et al., 2015). Maximisation of grain number was proposed as a means of managing the trade-off between yield potential and tolerance. Source-sink relationships were also used as an approach to understand tolerance traits (Collin et al., 2018) with no correlation found between tolerance and yield potential, meaning that high-yielding tolerant cultivars could be developed in breeding programs. The relationship between green leaf area duration and yield was also proposed as a means of characterising tolerance (Castro & Simón, 2016), with again no correlation and, hence, trade-off between tolerance and yield potential. Yield equations were used to calculate the contribution of tolerance to maximise actual yield of wheat given an effective fungicide programme (van den Bosch et al., 2022). Some cultivars were found to have yields close to the fully protected yield in the presence of the disease.

5.2 | Plant parasitic nematodes

In a general review, Dalmasso et al. (1992) define tolerance to plant parasitic nematodes as an adaptive mechanism for plants faced with multiple environmental stresses. Tolerant plants allow nematodes to develop and multiply but without sustaining significant yield loss. Fuller et al. (2008) review mechanisms of resistance to nematodes but without mentioning the early work on tolerance (Trudgill, 1991). In an evaluation of the most important plant parasitic nematodes (Jones et al., 2013), the value of plant tolerance as a means of control was only mentioned for root lesion nematodes (*Pratylenchus* spp) and the pine wilt nematode (*Bursaphelenchus xylophilus*) although earlier work on tolerance of the root knot nematodes (*Meloidogyne graminicola*) is cited. Much reported work with nematodes is concerned with responses to flooding and water management (Soriano et al., 2000; Tandingan et al., 1996). Interactions between nematodes and viruses in relation to resistance and wilting tolerance

to beet cyst nematodes and beet necrotic yellow vein virus was studied by Heijbroek et al. (2002) but no significant interaction between the types of resistance between nematode and virus was found.

5.3 | Oomycete pathogens

Very few recent studies have characterised tolerance to oomycete pathogens. In their review, Pagán and García-Arenal, (2018) give only one example, the downy mildew *Hyaloperonospora arabidopsidis* infecting the model plant *A. thaliana* and affecting seed and flower production. In a review of oomycete–plant host interactions, Fawke et al. (2015) discuss in detail R-gene resistance and S-gene susceptibility, in which susceptibility can be modified during the stages of infection, establishment, and sustenance during pathogenesis. Hence, susceptibility so modified can be considered partial, but no indication is given as to how this relates to tolerance and plant fitness. Previously with the interest in producing transgenic plants, approaches involving the over-expression of polyamide oxidase (PAL) in tobacco gave pre-induced tolerance against *Phytophthora parasitica* var. *nicotianae* by preventing plant colonisation (Moschou et al. 2009), so it is a moot point whether tolerance is an appropriate designation for this effect.

5.4 | Bacterial pathogens and mollicutes

Pagán and García-Arenal (2018) cite publications on *Xanthomonas campestris*, *X. viridiflava*, and *Pseudomonas syringae* as reporting tolerance of plant pathogenic bacteria, affecting seed production, chlorophyl content, symptoms, and mortality of *A. thaliana*. These studies were made in the 1990s and early 2000s. More recently, a study by Tan et al. (2014) on *X. campestris* and effector proteins in *Arabidopsis*, suggested that bacterial pathogens might have evolved effectors that initiate a disease tolerance that sustains plant fitness for a given pathogen burden and, hence, enhances their survival. As mentioned in an earlier paper on AN effects, an *Arabidopsis* mutant was found to confer tolerance of drought and *P. syringae* (Xie et al., 2020). A 20-year study on European stone fruit yellows disease of apricot (*Prunus armeniaca*) caused by *Candidatus* Phytoplasma prunorum showed that some initially diseased plants became symptomless but retained the phytoplasma (Osler et al., 2014). Buds from recovered and non-recovered plants were then grafted onto peach: 93% of the non-recovered grafts resulted in infection, but only 1.5% of recovered grafts, a result attributed to epigenetic change and acquired tolerance.

6 | A BROADER VIEW OF TOLERANCE

Plant disease tolerance is most often viewed from the perspective of the plant pathologist, a necessary but not sufficient perspective to appreciate the agronomic, environmental, and ecological factors of plant stress responses where a broader perspective is necessary.

6.1 | Agronomy and plant nutrition

In many studies the addition of nutrients to crops decreases the incidence of diseases, especially where there are nutrient deficiencies although where one is limiting addition of another may exacerbate disease. It is supposed that nutrients are involved in both resistance and tolerance (in the sense that the crop genotype grows and yields despite infection) (Dordas, 2009), although this is mostly reviewed without distinguishing between the two traits. Examples of where nutrient addition affects specifically tolerance are given in the review: decreasing levels of Si at high N rates affects tolerance in complex ways, Si is known to increase the tolerance of turfgrasses to several soil-borne and foliar fungal pathogens, Cl may increase the availability of Mn and increase tolerance, green manures and organic amendments more generally affect the availability of nutrients and in some cases the expression of tolerance. A contrast can be made between pathogens which are primarily N-limited to those primarily C-limited, but little is known of whether this contrast carries through to tolerance of the pathogens (Hoffland et al., 1999, 2000). Newton et al. (1998) manipulated fertilizer levels applied to reportedly tolerant and nontolerant spring barley genotypes to powdery mildew to determine whether tolerance (of disease) was a heritable or a physiological characteristic dependent on environmental conditions. As a criterion for classifying varieties as tolerant (or nontolerant) they used a regression line of percent yield loss against area under the disease progress curve (AUDPC), with varieties placed below (above) one standard deviation of the fitted line as tolerant (nontolerant). An ELISA-based biomass measure was also used and correlated positively and significantly with AUDPC. The relationship was then tested over 2 years with different fertilizer treatments. Results showed that although there were strong environmental interactions over years and fertilizer treatments, some genotypes showed stable tolerance and nontolerance traits,

indicating a heritable component that could be exploited in breeding varieties suited to certain environments. The form of N nutrient solution (different ratios of NH_4 to NO_3) altered disease tolerance to BYDV in glasshouse-grown wheat (expressed as primary tiller height) and oat (kernel weight) (Riedell, 1999). NH_4-containing fertilizers would not ameliorate grain yield loss to BYDV. In general, recent work on plant disease tolerance in relation to nutritional factors has been lacking.

6.2 | Interaction with abiotic stress tolerance

Abiotic stress tolerance has long been recognised as a target in plant breeding. The importance of combining heat tolerance for wheat in the tropics with disease resistance was noted by Dubin and Rajaram (1996). Interactions of abiotic and biotic stress can have subtle physiological effects affecting responses to stressors. Drought stress was found to increase the expression of resistance genes to *R. padi* in *Hordeum vulgare* and *Hordeum spontaneum*, with negative consequences for aphid fitness, thus affecting drought tolerance and aphid resistance (Leybourne et al., 2022). Strategies to combine tolerance to multiple abiotic and biotic stressors in the Cucurbitacaea by trait identification, germplasm screening for donor selection in conventional breeding, and direct genetic manipulation, have been proposed (Parvathi et al., 2022). Elevated levels of salicylic, jasmonic, and absisic acids in transgenic alfalfa (*Medicago sativa*) were associated with upregulated plant defence and abiotic stress response genes enhanced tolerance to fungal infection by *Colletotrichum trifolii* and drought (Gallego-Giraldo et al., 2011). Fungal endophytes confer tolerance for a range of biotic and a range of abiotic stressors and confer fitness benefits (Rodrigues et al., 2009). The role of beneficial microbes on initiating plant transduction pathways and drought tolerance has recently been reviewed (Shaffique et al., 2022; Suman et al., 2022). Cytokinins affect many growth, development and physiological traits and have been shown to affect biotic and abiotic stress tolerance. In *A. thaliana* challenged with tobacco mosaic virus, the bacterium *P. syringae*, and the necrotrophic fungus *Botrytis cinerea*, effects were manifested differently depending on the cytokinin, whether kinetin or benzyladenine (BA) (Bózso & Barna, 2021). BA had a much stronger protective effect on necrotic stress due to senescence-inhibition of BA-treated leaves.

Recent reviews (González et al., 2020; Prasad et al., 2022) have been made of studies looking at interactions between virus infection and abiotic stress tolerance: including water stress and drought, salinity, extreme heat, freezing, raised CO_2 levels, excess light, and oxidative stress. Interactions with plant associated microorganisms more generally have been reviewed in mitigating drought stress (Poudel et al., 2022). Virus infection can modify a plant's response to various abiotic stressors and conversely abiotic stressors can affect virus development within plants and disease progression in crops through effects on vector behavior (Vasquez et al., 2022). Despite the pathogenic nature of many plant–virus associations, there are examples where viruses have been shown to have beneficial effects in mitigating abiotic stress and supporting tolerance, in some cases in combination with other microbial associations (Omae & Tsuda, 2022; Table 3).

6.3 | Tolerance in populations of wild plants

Compared with crop plants the general effects of viruses on wild plants have been less investigated (Cooper & Jones, 2006; Malmstrom & Alexander, 2016; Shates et al., 2019). One reason may be that many viruses in wild plants are cryptic, leading to symptomless "latent" infection (Takahashi et al., 2019) which under some circumstances can be activated and result in symptoms. However, it remains a possibility that some viruses that are asymptomatic in adult plants induce higher mortality in younger plants compared with non-infected ones, hence the importance of choice of phenological stage in tolerance studies. The presence of disease with no loss in plant fitness may be a feature of wild plant populations (Alexander, 2010) with selection for tolerance one possible reason for the widespread occurrence of disease in some populations, at least in long-lived perennial shrubs (Roy et al., 2000). The point about perennial plants is important as the period of exposure to pathogens is much longer compared with annual plants (Susi & Laine, 2015).

It has been predicted that tolerance would be more common with native rather than introduced pathogens and may lead to an evolutionary stable state (Roy & Kirchner, 2000). This prediction was tested with *Senecio vulgaris* and the rust fungi *Coleosporium tassilaginis* (native) and *Puccinia lagenophorae* (introduced) in the United Kingdom (Inglese & Paul, 2006). Host growth and fitness per unit of infection (% area of sporulating rust pustules integrated over time) were less reduced with the native rather than introduced rust species, resulting from a smaller reduction of photosynthesis per unit of infection, both per leaf and for the whole plant.

Tolerance may also depend on the extent to which plant ecotypes are adapted to altitude, latitude, or other topographical features. Upland and lowland ecotypes of the prairie grass *Panicum virgatum* differed in their response to infection with BYDV (Alexander et al., 2017).

Virus infection in the upland ecotype reduced multi-year fitness by delaying the flowering period and reducing seed filling compared with the lowland ecotype. There was no indication that tolerance to the virus had associated effects on drought or herbivory responses. Release of virus-resistant plants in agricultural systems may pose threats to native plant ecosystems if wild host populations acquire novel resistance genes. This was examined in a model system of wild *Trifolium repens* infected with clover yellow vein virus (ClYVV) in southeast Australia (Godfree et al., 2009). ClYVV-infected wild *T. repens* had reduced fecundity, growth, and survival but the severity of these fitness costs depended on host tolerance to infection, isolate aggressiveness, and environmental heterogeneity. These impacts reduced population growth and the niche size of wild *T. repens* populations. Hence, release from virus infection through the acquisition of novel resistance genes from agricultural populations may have unintended consequences in wild plant communities.

7 | TOLERANCE AND DISEASE MANAGEMENT

Tolerance, defined conceptually as the ability of a plant to maintain yield in the presence of disease, has mostly been studied in single plant genotypes either alone or in monocultures. It can also be considered an attribute of crops grown in varietal mixtures or intercrops (Newton, 2016). Albeit that tolerance traits are often poorly defined even in monocultures, the question of how such traits interact, especially where there is wide variation among plants, is considered. It is proposed that "community" tolerance in this sense can only be assessed under sub-optimal field conditions rather than the optimal conditions usually ensured for controlled field trials. The authors also stress the significance of ecological tolerance provided not only by crop–crop interactions but also by the interactions with beneficial phyllosphere micro-organisms (Newton, 2016; Newton et al., 2010).

Management of plant viruses by means of deploying tolerant cultivars was reviewed by Seal et al. (2006) in the context of begomoviruses. Tolerance of viruses, other pathogens, and abiotic stress in fruit trees and rootstocks can be invaluable in disease management (Rodríguez-Verástegui et al., 2022). Tolerance may provide a resilience strategy for control of Sharka disease caused by plum pox virus (PPV) (Rimbaud et al., 2015). Cultivars considered tolerant exhibit few symptoms on fruits despite PPV infection. However, the virus is still able to multiply within plum hosts and be transmitted to other plants either through vectors or movement of plant material. The deployment of tolerant cultivars is not recommended in areas where the management strategy is to eradicate or suppress the disease and further is not compatible with the strategy of deploying cultivars with hypersensitive resistance because of the risk of resistance breakdown.

The impact of viruses on species composition in managed mixed species pastures depends on the fitness of individual plant species (Jones, 2022), their ability to grow, set seed, and persist in the pasture. In this, tolerance will play a major role: a plant species weakened by virus infection may not be able to compete with a virus-tolerant species, virus may spread from a tolerant species to a susceptible or less tolerant species causing decline, or there is no impact due to mild symptoms or asymptomatic infection across all species in the pasture, as shown schematically in Figures 4 and 5. Thus, disease management options for viruses in managed pastures should include phytosanitary controls of seed-borne viruses and suppression of virus spread by an appropriate balance of tolerant, resistant, and susceptible species in the mixed pasture, made difficult where there are multiple viruses and potential vectors present.

8 | MATHEMATICAL MODELS OF TOLERANCE

Mathematical models have been proposed as a means of analysing the dynamics of plant virus epidemics and evaluating disease management options (Jeger et al., 2004, 2018). Modelling tolerance mechanisms to plant diseases has not been a particularly active area of research and was not recognised in the 13 modelling challenges outlined by Cunniffe et al. (2015). There has been some modelling for plant viruses on evolutionary and epidemiological aspects of tolerance (Cronin et al., 2014; Hily et al., 2014; Moore et al., 2011; Sisterson & Stenger, 2018; van den Bosch et al., 2006; Zeilinger & Daugherty, 2013). Models have been proposed for fungal plant pathogens (e.g., Roy & Kirchner, 2010), animal diseases (e.g., Detilleux, 2011), or as representing more generic host–pathogen systems (e.g., Best et al., 2008).

Models of host defence mechanisms and other management options in relation to the potential for the evolution of plant viruses were developed by van den Bosch et al. (2006, 2007). One prediction of the models developed was that host defence through symptom reducing tolerance would place selection on the virus to increase its evolutionary stable state for within-plant virus multiplication. However, the context in these studies was for the vegetatively propagated crop cassava and cassava mosaic disease, and hence symptom-reducing tolerance, sometimes termed mortality tolerance rather than a reduction in fitness measured as plant fecundity and reproductive

TABLE 3 Examples of beneficial effects of plant viruses amongst other associated microbes in mitigating host abiotic stress. The studies are ordered alphabetically by the first author, rather than by crop or plant species.

Crop/plant species	Virus	Associated microbe	Abiotic stressor	Main finding/comment	Source
Nicotiana benthamiana/ *Arabidopsis thaliana*	Potato virus X/plum pox virus	none	drought	Virus infection increased drought tolerance, and, in some cases, viable progeny of *Arabidopsis thaliana* exposed to drought stress. However, more virulent viruses overcame any beneficial effects associated with increased drought tolerance.	Aguilar et al. (2017)
Winter cereals (Triticale, wheat, rye)	Barley yellow dwarf virus	*Typhula* spp	cold	Barley yellow dwarf virus tolerance increased the cold tolerance of rye and triticale during snow cover and exposure to snow molds, an important aspect contributing to yield stability.	Collin et al. (1997)
Wild *Nicotiana benthamiana*	Yellow tailflower mild mottle virus	*Cladosporium cladosporiodes*/ unidentified ascomycete	drought	Fungal endophytes and a tobamovirus confer water stress tolerance with a significant upregulation of drought-related genes. Endophytes and viruses affected the plant response to water stress similarly, but co-infection led to no additional effects.	Dastogeer et al. (2018)
Quinoa *Chenopodium quinoa*	Chenopodium quinoa mitovirus 1	none	drought	*Chenopodium quinoa* lines infected by mitovirus activate metabolic pathways that may confer drought tolerance	Di Silvestre et al. (2022)
Ginseng *Panex* spp	Unassigned cryptic viruses as endophytes	Endophytic fungi, archaea, and bacteria	general	Cryptic viruses and potential (unproven) role with other endophytes in abiotic stress tolerance in ginseng by reducing stress-related growth factors	Goodwin (2022)
Grapevine *Vitis vinifera*	Grapevine fanleaf virus	none	water deficit	The effects of mild water stress are better sustained by GFLV-infected rather than healthy vines. This effect was not apparent when the vines were subject to severe water stress.	Jež-Krebelj et al. (2022)
Arabidopsis thaliana	Turnip mosaic virus/cucumber mosaic virus	none	light intensity	TuMV multiplication and tolerance were increased under high light intensities leading to more efficient seed transmission, whereas CMV multiplication and tolerance were reduced with no effect on seed transmission.	Montes and Pagan (2019)

(Continues)

TABLE 3 (Continued)

Crop/plant species	Virus	Associated microbe	Abiotic stressor	Main finding/comment	Source
Nicotiana benthamiana/*Arabidopsis thaliana*	Turnip mosaic virus/cucumber mosaic virus	none	water deficit	Infection by TuMV or CMV promoted drought tolerance in both plant species. Infection of *N. benthamiana* by CMV improved reproductive fitness when exposed to drought. Water deficit did not affect seed transmission	Moreno et al. (2022)
Bromus hordeaceus/*Avena fatua*	Barley and cereal yellow dwarf viruses	Arbuscula mycorrhizal fungi	elevated CO_2	Under raised CO_2 an arbuscular mycorrhizal association increased virus titre of BYDV in two wild grass species and reciprocally virus infection increased mycorrhizal root colonization.	Rúa et al. (2013)
Nicotiana benthamiana	Tobacco mosaic virus	*Rhodopseudomonas palustris*	general	Beneficial phyllosphere bacteria used as biological control agents can improve plant tolerance to abiotic stress and have also been found to induce resistance to *Tobacco mosaic virus*	Su et al. (2019)

stage tolerance. In a similar vein, the model developed by Hily et al. (2014), combined both vector transmission and within host dynamics and considered tolerance as a factor in virus evolution.

The "reducing the fitness consequences of infection" concept for tolerance was used by Roy & Kirchner (2010). The governing equations were not presented except to say that the model was generic and most applicable to a systemic rust disease of long-lived plants. An equation was derived which gives the average fitness consequences of infection of different host types. On the assumption there are two phenotypes, a reference type and one with either resistance or tolerance, parameters are introduced to model the effects of resistance and tolerance in comparison with the reference type. Importantly resistance and tolerance were seen relative measures which can only be gauged against the reference phenotype. Resistance was modelled using a fractional reduction in the transmission rate; tolerance by a fractional decrease in the mean host life span when infected. In both cases, costs of resistance or tolerance (fractional reduction in the host growth rate) were modelled. The main conclusion drawn from the model was that in evolutionary terms the tolerant phenotype is likely to become fixed in the host population, whereas the resistant phenotype becomes polymorphic. Furthermore, implications are drawn by Roy and Kirchner (2010) on how mutualism can evolve from parasitism (see Hamelin et al., 2017) in cases where there is natural selection for tolerance mechanisms.

Compared with models that are posed in response to evolutionary questions, there are few which raise epidemiological concerns with most crop species or immediate ecological concerns with wild plant populations and communities. The success or otherwise of invading pathogens in establishing in a crop was modelled by Moore et al. (2011) for barley and cereal yellow dwarf viruses. A spatio-temporal model was developed to investigate whether a pathogen can facilitate the invasion of an exotic plant species, specifically BYDV and invasive non-native annual grasses. It was found that connectivity within the native perennial and invasive grass species, arrival time of the invasive plant species, and infection tolerance interacted to determine the success or failure of invasion, although no definition of the form of tolerance was given nor of which parameters were varied to incorporate different levels of tolerance (host fecundity or biomass). Cronin et al. (2014) introduce the concept of host development tempo (HDT), based on functional traits, and relate this to tolerance, where such hosts do not reduce vector and/or pathogen activity but rather have a greater capacity to acquire resources to acquire and allocate resources when infected. A structural equation model (see their Figure 1) was developed and applied to data on the BYDV/grass system. In this analysis, no resistance-tolerance trade-off was found.

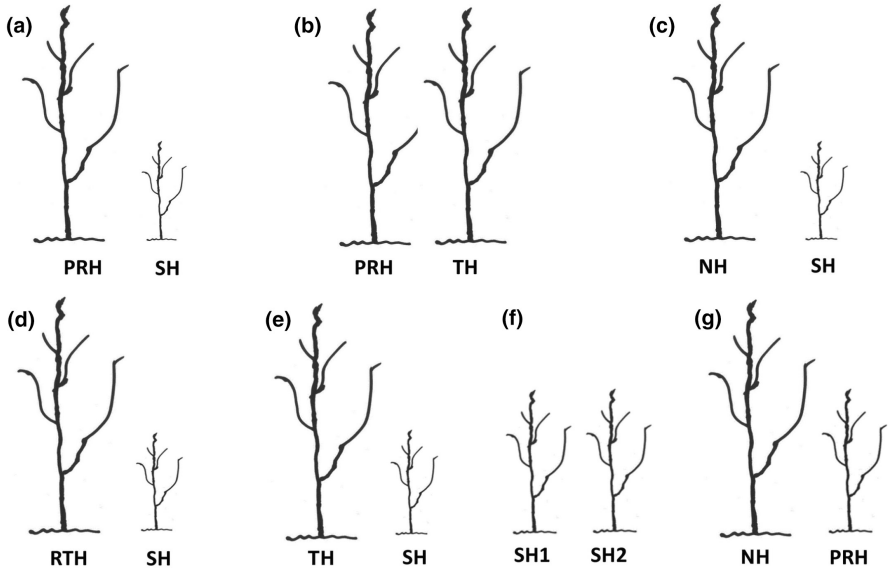

FIGURE 4 Schematic illustration of growth outcomes where virus infection was present in mixtures involving two plant species (Jones, 2022, Figure 4, re-used under creative commons attribution licence, with legend modified from the original). (a) a virus-infected, sensitive, susceptible host species (SH) is suppressed by competition with a partially resistant host species (PRH). (b) a virus-infected, tolerant host (TH) is unaffected by competition with a partially resistant host species (PRH). (c) a virus-infected, sensitive, susceptible host species (SH) is suppressed by competition with a nonhost species (NH). (d) a virus-infected, sensitive, susceptible host species (SH) is suppressed by competition with a relatively tolerant host species (RTH). (e) a virus-infected, sensitive, susceptible host species (SH) is suppressed by competition with a tolerant host species (TH). (f) Two susceptible host species each infected with the same two viruses but differing in their sensitivity to each virus (SH1 and SH2) are unaffected by competition. (g) a virus-infected, partially resistant host species (PRH) is partially suppressed by competition with a nonhost species (NH).

It was not possible however to resolve the role in HDT in determining tolerance, although it appeared that resistance played a greater role in the impact of infection on plant biomass.

Seasonal disease progress within a crop can be modelled with account taken of both host resistance and tolerance and can be used to determine the form of host defence best suited for different scenarios. Sisterson and Stenger (2018) compared the different outcomes of deploying partial resistance or tolerance in a perennial crop against a vector-borne disease. Tolerant plants were considered as having pathogen titres similar with those in susceptible plants but without the negative effects. Acquisition rates by vectors were assumed to be the same as from susceptible plants. By contrast, resistant plants were considered to have a lower virus titre and hence a lower probability of acquisition, although as the authors state the link between pathogen titre and vector acquisition is not always clear-cut. The system was modelled using a susceptible-exposed-infectious state model (SEIR) for both the susceptible and resistant host (where E represents the infected but not yet infectious state) and with inoculative or non-inoculative states defined for the vector. Only the effects of partial resistance were obtained with no distinction made between susceptible and tolerant plants as other aspects of tolerance were not modelled.

Another epidemiological issue that has arisen in the last decade is the effect of vector preferences for healthy or diseased plants. Such an effect has been shown in many laboratory-based studies but characterising this in the field in crop and vector populations has proved difficult. Disease dynamics when such preference is accounted for was modelled by Zeilinger and Daugherty (2013) in cases where either resistance or tolerance was present in the host population. The difference between the two defence traits was that acquisition cannot occur from resistant hosts but can from tolerant hosts. Hence, inoculative vectors have acquired virus from infected plants, either susceptible or tolerant, and can inoculate both classes and resistant plants. When vectors preferred infected plants, tolerance reduced disease incidence; when they avoided infected plants, tolerance increased disease incidence. Thus, the consequences for deploying resistant or tolerant plants depend on the form of vector preference if present.

How the epidemiology of disease-resistant and tolerant crops affects the behavior of growers and grower communities was modelled by Murray-Watson and Cunniffe (2022). It was concluded that tolerance only benefits those growers in the community who use it but may decrease yield for those who do not, whereas resistance benefits all because of reduced inoculum presence across

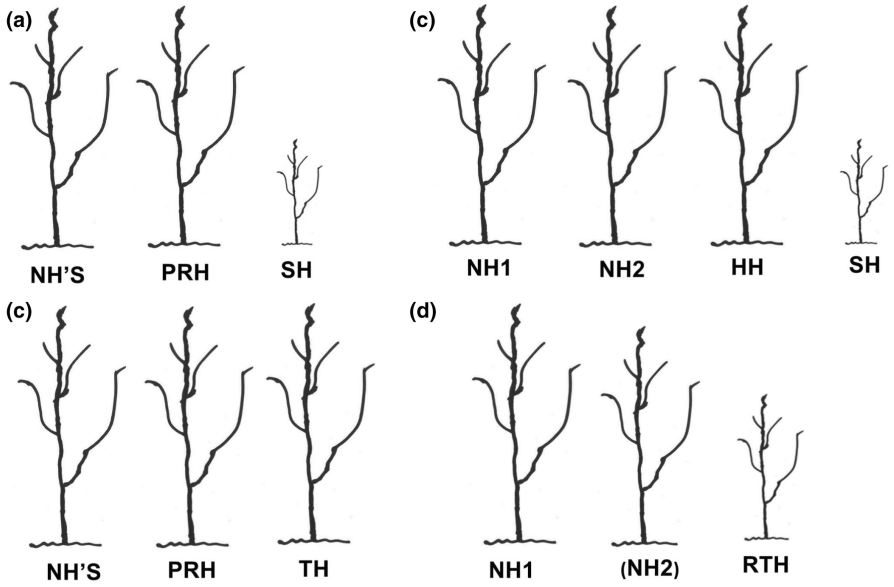

FIGURE 5 Schematic illustration of growth outcomes where virus infection was present in three or more plant species mixtures (Jones, 2022, Figure 5, re-used under creative commons attribution licence, with legend modified from the original). (a) a virus-infected, sensitive, susceptible host species (SH) is suppressed by competition with two nonhost species (NH'S) and a partially virus-resistant host species (PRH). (b) a virus-infected, tolerant, susceptible host species (SH) is unaffected by competition with two nonhost species (NH'S) and a partially resistant host species (PRH). (c) a virus-infected, sensitive, susceptible host species (SH) is suppressed by competition with two nonhost species (NH1 and NH2), and with healthy hosts of the same susceptible species (HH). (d) a virus-infected, relatively tolerant, susceptible host species (SH) is partially suppressed by competition with one of two nonhost species (NH1) but not by the second (NH2, denoted by parentheses).

the community but gives a "free-ride" to those who do not use it.

For animal diseases, a Markov Chain process was formulated in a susceptible-infected-susceptible (SIS) state model for bovine mastitis (Detilleux, 2011). The purpose was to investigate the distinct mechanisms of tolerance and resistance on damage caused by the pathogen. A scaling parameter acting against virulence (defined as the maximum loss in performance due to the pathogen) was used to represent tolerance. If there were fitness costs associated with tolerance, there would be little benefit in tolerance in cases where there was low pathogen virulence and transmissibility. However, in commercial settings higher levels of tolerance in individuals would be more beneficial than increased levels of resistance.

A generic model developed by Best et al. (2008) started with the view that tolerance limits the impact of disease at any pathogen burden and distinguished between mortality impacts of disease (mortality tolerance) and those acting on reproductive ability (sterility tolerance). An SIS state model was formulated which included an additional mortality term due to disease (virulence) α and a recovery from infection term γ. It was assumed that there is a trade-off such that a reduction in α (increased tolerance) causes a reduction in γ (reduced resistance), where the trade-off can take a convex, linear, or concave form. Simulation outputs of the evolutionary trajectories, using adaptive dynamics, shows that the population can move to either an intermediate level of mortality tolerance before branching to a state of high tolerance and minimal resistance, or one of high resistance and minimal tolerance. By contrast with sterility tolerance the population can evolve to co-existing hosts with high and low tolerance. More recent work following the same modelling approach (Ferris & Best, 2019) showed that temporarily fluctuating environments increases the host's investment in tolerance and shows qualitative distinction between resistance and tolerance evolution. Vitale & Best (2019) show paradoxically that by lowering tolerance (increasing disease induced mortality) pathogen/parasite extinction can be achieved.

9 | CONCLUSIONS

Despite the ambiguities and misunderstandings surrounding tolerance as a plant defence mechanism and its use for plant breeding, disease management, and crop improvement, there is increasing evidence for its importance including plant viruses, the main topic of this review. Much work is now emphasising the plant reproductive and survival fitness aspects of tolerance, although there is some debate over its interpretation for crops compared with wild plants. Much recent work on genetics and evolutionary aspects of tolerance has been done with model

plant systems, particularly *Arabidopsis*, in laboratory and microcosm experiments rather than in field-based studies with crops or wild plant populations. Field-based studies of tolerance have been done with barley and cereal yellow dwarf viruses and viruses of the *Cucurbitaceae*. However, there is a need to broaden the crop range, whether for crops in broad-acre monocultures, mixed horticultural systems, or in smallholder farming where the complex of crops, viruses, and vectors will differ as will disease epidemiology. It is important to assess the epidemiological consequences of growing tolerant crops across this diverse range of cropping systems. Beyond this there is a need to consider pathogen and disease tolerance as just one aspect of biotic stress that interacts more generally with abiotic stress in surprising ways, with sometimes beneficial rather than deleterious effects.

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