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Review

Plants, viruses and the environment: Ecology and mutualism

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ABSTRACT

Since the discovery of *Tobacco mosaic virus* nearly 120 years ago, most studies on viruses have focused on their roles as pathogens. Virus ecology takes a different look at viruses, from the standpoint of how they affect their hosts' interactions with the environment. Using the framework of symbiotic relationships helps put the true nature of viruses into perspective. Plants clearly have a long history of relationships with viruses that have shaped their evolution. In wild plants viruses are common but usually asymptomatic. In experimental studies plant viruses are sometimes mutualists rather than pathogens. Virus ecology is closely tied to the ecology of their vectors, and the behavior of insects, critical for transmission of many plant viruses, is impacted by virus–plant interactions. Virulence is probable not beneficial for most host–virus interactions, hence commensal and mutualistic relationships are almost certainly common, in spite of the paucity of literature on beneficial viruses.

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Introduction

Plants were the first known hosts for viruses (Beijerinck, 1898), and plant viruses have been a focus of research for nearly 120 years. Although early research on viruses was more ecological in nature, most of the work done in plant virology over the past fifty years has been molecular (vanderWant and Dijkstra, 2006). Ecology is a much older discipline than virology, but in the past ten years the subfield of virus ecology has emerged as we learn more about viruses in natural environments and how viruses deter or facilitate the success of a host's interaction with the environment (Malmstrom et al., 2011; Roossinck, 2013). It is clear from numerous lines of research that plants, viruses and the environment have been interacting for a very long time, and relationships have evolved that are very intricate and complex and include

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other microbes, insects, neighboring plants and herbivores, along with abiotic factors such as nutrients, water resources, heat and cold stress, and adverse soil conditions.

Until recently most research in plant virology focused on the disease-causing viruses in crops and ornamental plants, but metagenomic studies have shown that viruses are very abundant in wild plants, and these are generally asymptomatic [reviewed in Roossinck (2012b) and Roossinck et al. (in press)]. The role of viruses in wild plant populations is beginning to be understood; the dynamics of viruses in the invasiveness of introduced plants species is being characterized; and the remarkable details of insect–virus–plant relationships point to long-standing interactions among multiple partners.

In virus ecology we look at viruses as symbionts. Symbiosis is defined as two dissimilar entities living in or on one another in an intimate relationship (deBary, 1879). Symbionts fall on a continuum from pathogenic to mutualistic, and viruses can move among lifestyle choices depending on the environmental conditions of the host (Fig. 1).

This review will discuss the diversity of plant viruses from what we know about crop diseases to what is being discovered through metagenomic studies of wild plants; the complex role of insects in the plant–virus relationship; and the impacts of plant viruses on the evolution and ecology of their hosts.

Diversity and incidence of plant viruses

The impression from the ninth report of the International Committee for the Taxonomy of Viruses is that there are not very many viruses of plants. The report list just under 1000 different species (King et al., 2012). However, the vast majority of these are from crop plants, and recent studies of plant virus biodiversity using metagenomic approaches are revealing the abundance and novelty of plant viruses. Viruses are abundant in wild plants, from the tropics (Roossinck, 2012b) to Antarctica (Hopkins et al., 2014), with infection incidence as high as 60% based on current and older technologies, and most are turning out to be novel. In studies where samples are enriched for virus-like nucleic acids by various methods, as many as 90% of the resulting sequence reads have no similarity to anything in the public databases [recently reviewed in Roossinck et al. (in press)]. In addition to wild plants, plant virus-like nucleic acids have been found in numerous aquatic environments (Culley et al., 2006; Djigeng et al., 2009; Kim et al., 2008; Mehle and Ravnikar, 2012; Rosario et al., 2009; Tamaki et al., 2012), and in feces from humans and other animals (Li et al., 2010; Ng et al., 2014; Phan et al., 2011; Victoria et al., 2009; Zhang et al., 2006). This remarkable diversity, most of which is probably still unknown based on the current rate of novel findings, implies important roles for viruses in the evolution and ecology of their hosts. It also points to the need for more studies on virus biodiversity (Stobbe and Roossinck, 2014).

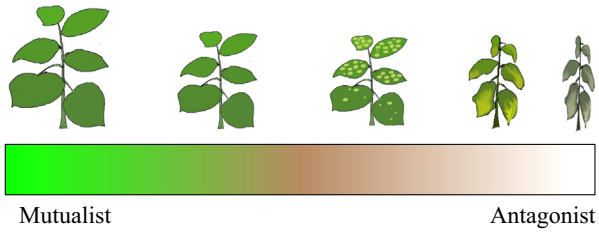

Fig. 1. Plant viruses on a symbiotic continuum. A virus infected plant may be benefited by virus infection (extreme left), or harmed by the virus to the point of death (extreme right). Viruses fall on a continuum of interactions between mutualism and antagonism, or pathogenesis, and these lifestyle choices change with changing environments.

Plants, insects and viruses: intimate relationships

Other than through seed dispersal most plants do not move across significant distances; hence their horizontally-transmitted viruses must be moved by others. Most often the vectors for plant viruses are insects, although below ground transmission also occurs through nematodes, chytrids or plasmodiophorids. The relationships among plants, insects and viruses are ancient, and it is not surprising that they are intimate and complex. Insects vectors are in turn colonized by other entities, and endosymbiotic bacteria produce compounds that are involved in plant virus transmission as well (Morin et al., 1999; vandenHeuvel et al., 1994). Although similar relationships with other vectors exist, they are less well studied and will not be considered here.

Insect transmission of plant viruses is usually categorized in four ways (Table 1), depending on how long the insect needs to feed to acquire the virus, how long it remains viruliferous, how long it must feed to transmit the virus, and whether or not the virus circulates through the insect gut and/or propagates in the insect [comprehensively reviewed in Bragard et al. (2013)]. These transmission modes affect the evolution of plant–virus–insect relationships.

Transmission by thrips

Thrips are tiny winged insects that in themselves can cause considerable damage to plants. The tospoviruses, members of the *Bunyaviridae*, are persistently transmitted by thrips. They propagate in the thrips vector, and are vertically transmitted in the insects as well, meaning that the transmission can occur for long periods of time and in later generations of the insects.

Plants respond to thrip damage by producing antifeeding compounds. Juvenile thrips fed on thrip-damaged pepper plants are negatively impacted compared to juveniles fed on healthy peppers. However, if the pre-feeding thrips are infected with the tospovirus *Tomato spotted wilt virus* (TSWV) the juveniles do better, similar to those on thrip-free plants. Mechanical inoculation of plants with TSWV results in the best outcome for juveniles, even better than clean plants. In nature all TSWV-infected plants will have been damaged by thrips: the virus ameliorates the negative effects of thrip damage so the virus is beneficial to the

Table 1
Major modes and characteristics of insect transmission.

Type of transmission	Acquisition time[a]	Retention time[b]	Transmission time[c]	Insects
Non-persistent	Minutes	Minutes to hours	Minutes	Aphids, thrips (*via* pollen)
Semi-persistent	Minutes to hours	Minutes to hours	Minutes to hours	Aphids, beetles, leafhoppers, mites, thrips, whiteflies
Circulative	Hours to days	Hours to days to life	Hours to days	Aphids, leafhoppers, treehoppers, whiteflies
Circulative-propagative	Hours to days	Days to life to generations	Days to life	Aphids, leafhoppers, mites, thrips, planthoppers,

[a] The time needed for the insect to acquire the virus.
[b] The time the insect remains viruliferous.
[c] The feeding time needed for the virus to be transmitted to the new host. In some cases longer feeding times result in more efficient transmission.

insect vector/host (Belliure et al., 2005). Thrip-damaged Arabidopsis plants produce jasmonic acid (JA), which is involved in the plants' resistance to thrips and probably explains why juveniles are negatively impacted. TSWV-infected plants produce salicylic acid (SA), which counteracts the JA response, and makes plants a better host of thrips (Abe et al., 2012). The positive response of insects on virus-infected plants can extend to other insects as well. TSWV infection and/or thrip damage affects spider mites; the spider mites do better on plants inoculated with virus *via* thrips, but thrip damage without virus does not have a negative effect on the spider mites, as it does on the thrips, rather the spider mites do better on these plants as well (Belliure et al., 2010).

Thrips infected with TSWV change their feeding behavior in comparison to uninfected thrips: males feed more, and importantly probe more in a way that does not damage the plant cell, the type of probing that is required for virus transmission. Female feeding is not affected. Although the females probe more often than males, virus transmission is considered to be mostly *via* male feeding because males are more heavily infected with the virus (Stafford et al., 2011). It is interesting that animal *Bunyaviridae* also affect insect vector feeding behavior. Mosquitoes carrying *La Crosse virus* show increased biting activity and refeeding on mammalian hosts (Jackson et al., 2012).

Transmission by aphids

Aphids are also small plant-feeding insects that are probably the best-studied of all the plant virus vectors. Some viruses such as *Cucumber mosaic virus* (CMV) are generalists in terms of transmission, and can be vectored by hundreds of different aphid species in a non-persistent manner (Palukaitis et al., 1992), whereas other viruses such as *Barley yellow dwarf virus* (BYDV) have a very specialized interaction with aphids and specific virus strains are transmitted by individual aphid species in a circulative manner (McElhany et al., 1995).

When given a choice, aphids are attracted to CMV-infected plants, but once they begin to feed the plants are induced to produce anti-feeding compounds. This moves the insects rapidly away from the plant to new hosts, a strategy that enhances the transmission of CMV, which only requires very brief feeding periods both for acquisition and transmission (Carmo-Sousa et al., 2014; Mauck et al., 2010). This work led to the hypothesis that viruses can induce volatiles that attract insect vectors, but the persistently-transmitted viruses induce profeeding behavior as well, while the nonpersistently-transmitted viruses induce anti-feeding behavior to rapidly move vectors off once the virus is acquired (Mauck et al., 2012).

Although CMV is considered a generalist because it has been reported to infect 1200 species of plants, in fact field isolates are still somewhat specialized in terms of their effects on vectors. In another study, a field isolate of CMV from squash did not show the same aphid attraction and dispersal in pepper, and a field isolate from pepper showed reduced ability to attract and disperse aphids in squash, indicating that specialization occurs in the field, and highlighting the ability of RNA viruses to rapidly adapt to their local environment (Mauck et al., 2014).

Using *Potato virus Y* (PVY), a non-persistent aphid transmitted potyvirus, Kersch-Becker et al. tested the effect of virus infection in tomato on aphids and two other herbivores: the cabbage looper caterpillar and the Colorado potato beetle. Using three different strains of PVY they showed that the aphids and the other herbivores did better on virus-infected plants but to differing degrees with the different strains. The herbivore response was correlated to the levels of SA. PVY elicits an SA response in tomato that suppresses the plant defenses against chewing insects, although SA can activate defenses against some herbivores (Kersch-Becker and Thaler, 2014).

Cauliflower mosaic virus (CaMV) is a plant pararetrovirus that is non-persistently transmitted by aphids. CaMV is acquired by aphids through specialized transmission bodies that form within the infected plant cells. When an aphid vector begins feeding on the plant the transmission body rapidly becomes activated, facilitating uptake of the virus by the aphid. Hence the virus can "sense" the aphid vector to enhance its spread (Martinière et al., 2013). This intriguing mechanism, or related strategies, may be used by other viruses, but has not been studied as yet (Blanc et al., 2011). For example, *Tobacco mosaic virus* (TMV) is spread mechanically through wounding, hence almost any herbivore can serve as a vector. Wounding in plants releases volatile signals that cue neighboring plants to mount a response that can include resistance to bacterial pathogens. In an interesting study on wounding response, Dorokhov et al. (2013) showed that wound–response volatiles increased the gating capacity (*i.e.* cell-to-cell movement) and reproduction of TMV, perhaps setting the stage for enhanced TMV transmission (Gutiérrez et al., 2013).

BYDV is a member of the *Luteoviridae*, viruses that are limited to the phloem tissue of plants. This location means that aphids must probe long enough to reach the phloem during both acquisition and transmission of the virus, and the *Luteoviridae* are transmitted in circulative manner (Table 1). Aphids that have acquired BYDV through *in vitro* feeding prefer uninfected plants, whereas aphids that have been fed *in vitro* without BYDV prefer infected plants, facilitating the spread of the virus to uninfected plants (Ingwell et al., 2012). In a study with another member of the *Luteoviridae*, *Potato leafroll virus* (PLRV), non-viruliferous aphids also settled preferentially on virus-infected plants, while viruliferous insects preferred non-infected plants. This could be duplicated by using volatile organic compounds trapped from the headspace of infected and uninfected plants, showing that the insect is reacting to volatiles released from the plants upon virus infection (Rajabaskar et al., 2014). The attraction of aphids to PLRV-infected plants is further dependent on the age of the plant at inoculation, so plants inoculated at a later stage (five weeks after transplanting) had lower levels of aphid arrestment than mock-inoculated plants, as compared to those inoculated at a younger stage (one or three weeks after transplanting) where infected plants attracted more aphids (Rajabaskar et al., 2013).

Pea enation mosaic virus (PEMV) is an unusual member of the *Luteoviridae*. It is a chimeric virus, with RNA 1 containing a typical luteovirus genome and RNA 2 a partial genome of an umbravirus. The addition of the umbravirus movement protein on RNA 2 means that unlike other members of the family, PEMV is not phloem limited although its transmission is still circulative. Using PEMV and a true luteovirus, *Bean leaf roll virus* (BLRV), Wu et al. compared the settling preference and reproduction potential of pea aphids on virus infected peas. Aphids were given the choice of PEMV or BLRV infected plants, PEMV or mock-infected plants, and BLRV or mock-infected plants. The aphids chose virus infected plants over mock-infected plants, and showed no preference between PEMV or BLRV. Using volatiles from the plant headspaces as orienting devices the aphids made the same selections. However, the reproductive rates of aphids were highest on BLRV-infected plants, followed by mock-infected plants, and lowest on PEMV-infected plants (Wu et al., 2014). Hence virus infection enhances the attractiveness of a plant to aphids, but the effect on the aphids varies from one virus to the next.

In another study, differences in aphid performance on PEMV-infected peas and beans were correlated with the age of the plant, although aphids showed a strong preference for virus-infected peas. Forced overcrowding also led to the formation of more winged aphids on PEMV-infected plants than on mock infected

plants (Hodge and Powell, 2009); increased aphid movement enhances virus spread to other plants.

The presence of additional insects can play an important role in virus transmission. Aphids can be colonized by parasitoids, and plant viruses can impact this relationship. Using *Turnip yellows virus*, another member of the *Luteoviridae*, Calvo et al. found that parasitized and non-parasitized aphids had equal transmission rates, but viruliforous aphids had a negative impact on success of the parasitoid, compared with nonviruliforous insects. However, when the time lag between acquiring the virus and exposure to the parasitoid was greater than 24 h the parasitoid success was not affected (Calvo and Fereres, 2011).

Bean yellow mosaic virus (BYMV) is transmitted non-persistently by aphids. Pea aphids settled more rapidly on BYMV-infected peas, but settling was reduced in the presence of a hymenopteran parasitoid of aphids. However, the presence of the parasitoid increased virus infection rates by nine fold, probably due to the increased movement of the aphids (Hodge et al., 2011).

Other viruses may also benefit from the responses to insects that increase vector transmission. *Zucchini yellow mosaic virus* (ZYMV) and *Watermelon mosaic virus* (WMV) are two potyviruses that can often be found in mixed infections on cucurbits. In single infections WMV does not elicit the strong aphid vector attraction effects that ZYMV does. However, on squash WMV replicates poorly in mixed infection but still benefits from the increased transmission elicited by ZYMV (Salvaudon et al., 2013).

Transmission by whiteflies

Geminiviruses are DNA viruses of plants that have been emerging rapidly around the world. Many of the geminiviruses are transmitted by whiteflies, most commonly specific biotypes of *Bemesia tabaci*, in a circulative manner, and spread of these insects has been largely responsible for the virus emergence. These relationships too are quite complex. In some cases the viruses and vectors have a mutualistic relationship, resulting in increased longevity and fecundity of the insects, while in other cases the viruses are antagonistic to the vectors; differences have led to increased invasiveness of some whiteflies (Jiu et al., 2007; Mann et al., 2008; Pan et al., 2013). Recently some of these differences have been attributed to yet another player, a bacterial endosymbiont of the insect vector (Su et al., 2013). These interactions also involve plant volatile compounds, and may include the subviral satellites of geminiviruses (Zhang et al., 2012). For example, tobacco is a poor host for whiteflies, but its host quality is improved by infection with the geminivirus *Tomato yellow leaf curl China virus*; synthesis of terpenoids, an insect repellent that is induced in whitefly infested plants, is attenuated by the virus infection (Luan et al., 2013).

The story of plants, insects and viruses would not be complete without mention of the interactions that involve insect viruses. Some reoviruses of plant-feeding insects use the plants as their vector. The viruses do not replicate in the plants, but are transmitted horizontally through the insects feeding on the plants and depositing virus that is later acquired by fresh insects (Noda and Nakashima, 1995). In the rosy apple aphid, infection with a densovirus (a DNA virus) induces a winged morph, whereas uninfected insects are larger, wingless, and have higher fecundity. The infected aphids deposit the virus in the plant tissue while feeding, but the virus does not replicate in the plants, so its levels remain low. Uninfected offspring of the infected winged insects establish colonies on these plants, until, eventually, a nymph acquires the virus from the plant tissue, develops into an infected winged morph, and moves off to establish a colony on a new plant (Ryabov et al., 2009). Hence the virus facilitates movement of aphids only when the host plant becomes too crowded.

Plant virus ecology is intimately tied to the ecology of the vectors, and the ecology of insects is also impacted by plant pathogens (Tack and Dicke, 2013). Recent years have demonstrated a remarkable array of ways that viruses influence the behavior of their vectors. A careful look at how insect–plant relationships have molded virus evolution will undoubtedly yield another dimension to the story (Gutiérrez et al., 2013).

Viruses and host evolution

The role of viruses in the evolution of life has been explored in depth in many recent publications (Forterre and Prangishvili, 2013; Koonin and Dolja, 2014; Villarreal and Ryan, 2011; Villarreal, 2005; Villarreal and Witzany, 2010). In addition to the ancient relationships between viruses and hosts that have molded aspects of host immunity and response to viruses, the number of virus-like sequences found in eukaryotic genomes reveals the existence of other ancient relationships that are, as yet, not understood. Here I will provide a few highlights of recent data from plant viruses.

Ecologists have done extensive studies on genotype versus environment, or G X E effects, and although disease has been thought to be important in the genotype diversity, the evidence for this minimal. One study using *White clover mosaic virus* (WClMV) on a variety of white clover genotypes found that the virus had a negative impact on all genotypes but the degree of impact varied greatly from one genotype to another, providing empirical evidence that a virus in the environment can effect the genotypic diversity or G X E (vanMölken and Stuefer, 2011). Hence while host diversity can impact the incidence and outcome of virus infection in plants (Roossinck and García-Arenal, 2015), viruses also can impact the degree of host diversity.

Endogenous viruses

The genomics era has revealed an abundance of viruses in many genomes, and plants are no exception. Integration of plant pararetroviruses has been known for a long time, as well as the presence of retrotransposons that were likely originally derived from viruses. Recent data shows that plant genomes have an abundance of these and other endogenous viral elements, including ones derived from both nuclear and cytoplasmic viruses. Geminivirus sequences were discovered in several *Nicotiana* genomes many years ago (Ashby et al., 1997). More recently, cytoplasmic RNA viruses have been found integrated in plant genomes (Chiba et al., 2011; Kondo et al., 2013; Liu et al., 2010). In many cases these integrated elements are transcriptionally active, implying a possible function for these genes. Overall the flow of genes is from viruses to host cells, and not the other way around (Koonin and Dolja, 2014) and viruses have ultimately been the source of many host genes.

The badnavirus *Banana streak virus* (BSV) is a pararetrovirus and a member of the *Caulimoviridae* that is endogenized in banana genomes, but can be released as an active virus by various types of stress. Abiotic stress such as temperature extreme, drought or wounding, crossing different banana species, and growing banana in tissue culture, can all result in release of the integrated virus into an active exogenous form. BSV developed into a major problem when tissue culture propagation of banana became popular. There are three "species" of eBSV that can exogenize. It is not known how or why integration occurs as it is not required for virus replication, unlike most retroviruses, which require integration into host DNA to replicate (Iskra-Caruana et al., 2010). Endogenization may be selected for as a method of immunization, as is seen with other endogenous

pararetroviruses in tomato (Staginnus et al., 2007) and petunia (Noreen et al., 2007).

The discovery of many virus sequences in genomes has led to the new field of paleovirology (Katzourakis, 2012). In addition to shaping host evolution, these ancient viral sequences, or genetic fossils, are being used to investigate the deeper evolution of viruses.

Persistent plant viruses

The so-called cryptic viruses of plants were first described in the 1980s (Boccardo et al., 1987), but very little attention has been paid to them. These viruses have a persistent lifestyle, in that they remain with their hosts for many generations, and are strictly vertically transmitted at near 100% rates (Roossinck, 2012a). In wild plants these viruses are the dominant type of virus found, with members of the family *Partitiviridae* being the most common (Roossinck, 2012b), but they are also common in crop plants. They are related to viruses that are found in fungi (Roossinck, 2014), and there is phylogenetic evidence from the partitiviruses and the endornaviruses that they rarely may be transmitted between plants and fungi (Roossinck, 2010; Roossinck et al., 2011). Parasites that have 100% vertical transmission are often assumed to be mutualistic, although the relationship between plants and their persistent viruses is not well understood. In one case, a partitivirus in white clover was shown to be mutualistic, suppressing nodulation in the plant when adequate nitrogen was present (Nakatsukasa-Akune et al., 2005). Detailed studies of the evolution of plant–persistent virus relationships are still lacking.

Viral impacts on plant ecology

Viruses may impact plants in both positive and negative ways. Although most studies in virology have focused on pathogens, a broader look reveals more intricate and stable interactions, especially in wild plant communities. Numerous factors can impact the prevelance and dispersal of viruses and the degree of disease that viruses induce. These can in turn affect the health and diversity of plant communities.

Viruses in wild plant communities

A number of studies have looked at the role of the luteovirus BYDV/*Cereal yellow dwarf virus* (CYDV) complex in grasslands in North America, where the prevalence of virus is shaped by interactions within the plant community and among plants, insects, herbivores, and abiotic factors (Power et al., 2011). The composition of wild grassland plant communities has a significant impact on the spread of the BYDV/CYDV complex (Moore and Borer, 2012; Moore et al., 2011). Viruses also play a role in species invasions (Rúa et al., 2011). In the Palouse grasslands of Washington and Idaho, the invasive African wiregrass (*Ventenata dubia*) is infected by BYDV and can act as a source of infection for native grasses (Ingwell and Bosque-Pérez, 2014). Studies on California grasslands have shown that invasive species can enhance the spread of BYDV/CYDV by attracting more aphids to the area that then spread virus to the more susceptible native grasses, causing loss of native grasses and enhances invasion by exotics (Malmstrom et al., 2005a, 2005b). The dynamics of viruses within the complex is affected by soil nutrients. In oats grown across nitrogen (N) and phosphorous (P) nutrient gradients CYDV prevalence is reduced in low N, high P soils, and BYDV outcompeted CYDV in co-infections, but when N was high this interaction disappeared. Hence the nutrient status of the host plants affects infection rates and competition among viruses (Lacroix et al., 2014). In a 2000 km north–south transect in the western United States and Canada, coinfection by four viruses in the BYDV/CYDV complex varied by latitude, and difference in virus prevalence varied by levels of abiotic stress (Seabloom et al., 2010).

In three populations of wild gourd, infection by CMV or ZYMV had varying impacts. ZYMV decreased population growth rate in one population, had no effect in another, and increased population growth rate in a third population. For CMV, infection reduced the population growth rate of two populations and had no effect on the third. In an experimental study, fruit and seed production were not altered by either virus, indicating that more complex factors are involved in the role of viruses in natural population growth rates, including the possible selection of tolerant genotypes (Prendeville et al., 2014).

Viruses in domestic and managed plant communities

The proposed use of native switchgrass for biofuels has led to improved varieties with greater biomass and/or digestibility. In a test of several stands in Michigan, those that were near wildtype had lower incidence of BYDV/CYDV than the improved varieties, and this could be reproduced in greenhouse studies. BYDV/CYDV does not cause significant disease in switchgrass, but high levels of virus could result in excessive spillover into nearby crops such as corn where the virus can have a significant impact (Schrotenboer et al., 2011).

Pepper golden mosaic virus and *Pepper huasteco yellow vein virus* are two geminiviruses that infect wild pepper (chiltepin) in Mexico. Although the plant is wild the fruit is edible, and an important part of the local diet. The plant is sometimes managed in semi-wild stands, and it is also cultivated. The heterogeneity of the plant genotypes is greatest in wild stands, and least in the cultivated stands. Virus incidence is greatest in the cultivated stands with low diversity, and lowest in the wild stands; hence plant population variation is critical to keeping virus levels low (Rodelo-Urrego et al., 2013). The link between biodiversity and virus disease incidence has been suggested for some time but few actual case studies have been done (Roossinck and García-Arenal, 2015). In the chiltepin, in addition to the lower incidence of virus infection, the level of disease in the infected wild plants is lower than in the cultivated plants (Rodelo-Urrego et al., 2013). The reason for this is not known, but, in general, disease symptoms are rare in virus-infected wild plants (Roossinck, 2012b).

Mutualistic relationships

Plant viruses can have positive impacts on their hosts in several ways. In some cases viruses enhance the ability of plants to counteract abiotic stress, in other examples viruses alter the plants ability to cope with biotic stress. In most cases, the benefits are conditional, for example while a virus may be a pathogen under normal conditions, it can be beneficial under stress (Bao and Roossinck, 2013).

Several plant viruses (CMV, TMV, *Tobacco rattle virus*, and *Brome mosaic virus*) were able to confer drought tolerance to a number of plants, and CMV conferred cold tolerance to beets in greenhouse studies (Xu et al., 2008). White clover plants infected with WClMV are less attractive to fungal gnats, probably due to the production of volatiles like β-carophyllene (vanMolken et al., 2012). In wild gourds, the bacterial pathogen *Erwinia trachiephila* causes wilt disease, and induces the production of volatiles that attract the beetle vector to the plant and induce movement to healthy plants. When these plants are infected with ZYMV, the beetle-attracting volatiles are reduced protecting the plants from the bacterial pathogen (Shapiro et al., 2012, 2013). Whether or not these benefits outweigh the costs varies, and depends on numerous environmental factors (Bao and Roossinck, 2013). Like all

symbiotic interactions, plant–virus relationships lie on a continuum between mutualism and antagonism (Fig. 1) and the placement on this continuum is by no means static.

Examples of mutualistic plant viruses are sparse, most likely because there has been a bias in the literature stemming from the earliest days of virology, that viruses are always pathogens. We now know that this is not necessarily the case, and further examples of viral mutualism are being described from many different systems (Barr et al., 2013; Roossinck, 2011; Virgin, 2014). Undoubtedly more will be found in plants as well.

Conclusions

Our knowledge about plant viruses is rapidly expanding in this metagenomic era. Viruses are abundant and extremely diverse in plants. Plant viruses are important factors in all aspects of a plants interaction with its environment. As no plant is an island, interactions include many additional players, including fungi, bacteria, insects, other plants, and the abiotic components of the plants environment. Recent studies on plant–virus–vector interactions show how viruses can manipulate the insects that facilitate their spread in ways that are as varied as the viruses themselves.

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References

Abe, H., Tomitaka, Y., SHimoda, T., Seo, S., Sakurai, T., Kugimiya, S., Tsuda, S., Kobayashi, M., 2012. Anatagonistic plant defense system regulated by phytohormones assists interactions among vector insect, thrips and a tospovirus. Plant Cell Physiol. 53, 204–212.

Ashby, M.K., Warry, A., Bejarano, E.R., Khashoggi, A., Burrell, M., Lichtenstein, C.P., 1997. Analysis of multiple copies of geminiviral DNA in the genome of four closely related *Nicotiana* species suggest a unique integration event. Plant Mol. Biol. 35, 313–321.

Bao, X., Roossinck, M.J., 2013. A life history view of mutualistic viral symbioses: quantity or quality for cooperation? Curr. Opin. Microbiol. 16, 514–518.

Barr, J.J., Auro, R., Furlan, M., Whiteson, K.L., Erb, M.L., Pogliano, J., Stotland, A., Wolkowicz, R., Cutting, A.S., Doran, K.S., Salamon, P., Youle, M., Rohwer, F., 2013. Bacteriophage adhering to mucus provide a non-host-derived immunity. Proc. Natl. Acad. Sci. U. S. A. 110, 10771–10776.

Beijerinck, M.W., 1898. Concerning a contagium vivum fluidum as cause of the spot disease of tobacco leaves. In: Johnson, J. (Ed.), Classics, vol. 7. American Phytopathological Society, St. Paul, pp. 33–52.

Belliure, B., Janssen, A., Maris, P.C., Peters, D., Sabelis, M.W., 2005. Herbivore arthropods benefit from vectoring plant viruses. Ecol. Lett. 8, 70–79.

Belliure, B., Sabelis, M.W., Janssen, A., 2010. Vector and virus induce plant responses that benefit a non-vector herbivore. Basic Appl. Ecol. 11, 162–169.

Blanc, S., Uzest, M., Drucker, M., 2011. New research horizons in vector-transmission of plant viruses. Curr. Opin. Mirobiol. 14, 483–491.

Boccardo, G., Lisa, V., Luisoni, E., Milne, R.G., 1987. Cryptic plant viruses. Adv. Virus Res. 32, 171–214.

Bragard, C., Caciagli, P., Lemaire, O., Lopez-Moya, J.J., MacFarlane, S., Peters, D., Susi, P., Torrance, L., 2013. Status and prospects of plant virus control through interference with vector transmission. Ann. Rev. Phytopathol. 51, 177–201.

Calvo, D., Fereres, A., 2011. The performance of an aphid parasitoid is negatively affected by the presence of a circulative plant virus. BioControl 56, 747–757.

Carmo-Sousa, M., Moreno, A., Garzo, E., Fereres, A., 2014. A non-persistently transmitted-virus induces a pull–push strategy in its aphid vector to optimize transmission and spread. Virus Res. 186, 38–46.

Chiba, S., Kondo, H., Tani, A., Saisho, D., Sakamoto, W., Kanematsu, S., Suzuki, N., 2011. Widespread endogenization of genome sequences of non-retroviral RNA viruses into plant genomes. PLoS Pathog. 7, e1002146.

Culley, A.I., Lang, A.S., Suttle, C.A., 2006. Metagenomic analysis of coastal RNA virus communities. Science 312, 1795–1798.

deBary, H.A., 1879. Die Erscheinung der Symbiose, Strasburg (listed as privately published).

Djigeng, A., Kuzmickas, R., Anderson, N.G., Spiro, D.J., 2009. Metagenomic analysis of RNA viruses in a fresh water lake. PLoS One 4, e7264.

Dorokhov, Y., Komarova, T.V., Petrunia, I.V., Frolova, O.Y., Pozdyshev, D.V., Gleba, Y.Y., 2013. Airborne signals from a wounded leaf facilitate viral spreading and induce antibacterial resistance in neighboring plants. PLoS Pathog. 84, e1002649.

Forterre, P., Prangishvili, D., 2013. The major role of viruses in cellular evolution: facts and hypotheses. Curr. Opin. Virol. 3, 558–565.

Gutiérrez, S., Michalakis, Y., VanMunster, M., Blanc, S., 2013. Plant feeding by insect vectors can affect ife cycle, population genetics and evolution of plant viruses. Funct. Ecol. 27, 610–622.

Hodge, S., Hardie, J., Powell, G., 2011. Parasitoids aid dispersal of a nonpersistently transmitted plant virus by disturbing the aphid vector. Agric. For. Entomol. 13, 83–88.

Hodge, S., Powell, G., 2009. Conditional facilitation of an aphid vector, *Acyrthosiphon pisum*, by the plant pathogen, pea enation mosaic virus. J. Insect Sci. 10, 155.

Hopkins, D.W., Swanson, M.M., Taliansky, M.E., 2014. What do we know about viruses in terrestrial Antarctica?. In: Cowan, D.A. (Ed.), Antarctic Terrestrial Microbiology. Springer-Verlag, Berlin, pp. 79–90.

Ingwell, L.L., Bosque-Pérez, N.A., 2014. The invasive weed *Ventenata dubia* is a host of *Barley yellow dwarf virus* withe implicatins for an endangered grassland habitat. Weed Res. 55, 62–70.

Ingwell, L.L., Eigenbrode, S.D., Bosque-Pérez, N.A., 2012. Plant viruses alter insect behavior to enhance their spread. Sci. Rep. 2, 578.

Iskra-Caruana, M.-L., Baurens, F.-C., Gayral, P., Chabannes, M., 2010. A four-partner plant–virus interaction: enemies can also come from within. Mol. Plant–Microbe Interact. 23, 1394–1402.

Jackson, B.T., Brewster, C.C., Paulson, S.L., 2012. La Crosse virus infection alters blood feeding behavior in *Aedes triseriatus* and *Aedes albopictus* (Diptera: Culicidae). J. Med. Entomol. 49, 1424–1429.

Jiu, M., Zhou, X.-O., Tong, L., Xu, J., Yang, X., Wan, F.-H., Liu, S.-S., 2007. Vector–virus mutualism accelerates population increase of an invasive whitefly. PLoS One 2, e182.

Katzourakis, A., 2012. Paleovirology: inferring viral evolution from host genome sequence data. Philos. Trans. R. Soc. B 368, 20120493.

Kersch-Becker, M.F., Thaler, J.S., 2014. Virus strains differentially induce plant susceptibility to pahid vectors and chewing hervibores. Oecologia 174, 883–892.

Kim, K.-H., Chang, H.-W., Nam, Y.-D., Hog, S.W., Kim, M.-S., Sung, Y., Jeon, C.O., Oh, H.-M., Bae, J.-W., 2008. Amplification of uncultured single-stranded DNA viruses from rice paddy soil. Appl. Environ. Microbiol. 74, 5975–5985.

King, A.M.Q., Adams, M.J., Carstens, E.B., Lefkowitz, E.J., 2012. Virus Taxonomy Ninth Report of the International Committee on Taxonomy of Viruses. Elsevier Academic Press, San Diego, CA p. 1327.

Kondo, H., Hirano, S., Chiba, S., Andika, I.B., Hirai, M., Maeda, T., Tamada, T., 2013. Charcterization of burdock mottle virus, a novel member of the genus *Benyvirus*, and identification of benyvirus-related sequences in the plant and insect genomes. Virus Res. 177, 75–86.

Koonin, E.V., Dolja, V.V., 2014. Virus world as an evolutionary network of viruses and capsidless selfish elements. Microbiol. Mol. Biol. Rev. 78, 278–303.

Lacroix, C., Seabloom, E.W., Borer, E.T., 2014. Environmental nutrient supply alters prevalence and weakens competitive interactions among coinfecting viruses. New Phytol. 204, 424–433.

Li, L., Victoria, J.G., Wang, C., Jones, M., Fellers, G.M., Kunz, T.H., Delwart, E., 2010. Bat guoano virome: predominance of dietary viruses from insects and plants plus novel mammalina viruses. J. Virol. 84, 6955–6965.

Liu, H., Fu, Y., Jiang, D., Li, G., Xie, J., Cheng, J., Pend, Y., Ghabriel, S.A., Yi, X., 2010. Widespread horizontal gene transfer from double-stranded RNA viruses to eukaryotic nuclear genomes. J. Virol. 84, 11879–11887.

Luan, J.-B., Yao, D.-M., Zhang, T., Walling, L.L., Yang, M., Wang, Y.-J., Liu, S.-S., 2013. Suppression of terpenoid synthesis in plants by a virus promotes its mutualism with vectors. Ecol. Lett. 16, 390–398.

Malmstrom, C.M., Hughes, C.C., Newton, L.A., Stoner, C.J., 2005a. Virus infection in remnant native bunchgrasses from invaded California grasslands. New Phytol. 168, 217–230.

Malmstrom, C.M., McCullough, A.J., Johnson, H.A., Newton, L.A., Borer, E.T., 2005b. Invasive annual grasses indirectly increase virus incidence in California native perennial bunchgrasses. Oecologia 145, 153–164.

Malmstrom, C.M., Melcher, U., Bosque-Pérez, N.A., 2011. The expanding field of plant virus ecology: historical foundations, knowledge gaps, and research directions. Virus Res. 159, 84–94.

Mann, R.S., Sidhu, J.S., Butter, N.S., Sohi, A.S., Sekhon, P.S., 2008. Performance of *Bemisia tabaci* (Hemiptera: Aleyrodidae) on healthy and *Cotton leaf curl virus* infected cotton. Fla. Entomol. 91, 249–255.

Martinière, A., Bak, A., Marcia, J.-L., Lautredou, N., Gargani, D., Doumayrou, J., Garzo, E., Moreno, A., Fereres, A., Blanc, S., Drucker, M., 2013. A virus responds instantly to the presence of the vector on the host and forms transmission morphs. eLIFE 2, e00183.

Mauck, K., Bosque-Pérez, N.A., Eigenbrode, S.D., DeMoraes, C.M., Mescher, M.C., 2012. Transmission mechanisms shape pathogen effects on host–vector interactions: evidence from plant viruses. Funct. Ecol. 26, 1162–1175.

Mauck, K.E., DeMoraes, C.M., Mescher, M.C., 2010. Deceptive chemical signals induced by a plant virus attract insect vectors to inferior hosts. Proc. Natl. Acad. Sci. U. S. A. 107, 3600–3605.

Mauck, K.E., DeMoraes, C.M., Mescher, M.C., 2014. Evidence of local adapation in plant virus effects on host–vector interactions. Integr. Comp. Biol. 54, 193–209.
McElhany, P., Real, L.A., Power, A.G., 1995. Vector preference and disease dynamics: a study of barley yellow dwarf virus. Ecology 76, 444–457.
Mehle, N., Ravnikar, M., 2012. Plant viruses in aqueous environment—survival, water mediated transmission and detection. Water Res. 46, 4902–4917.
Moore, S.M., Borer, E.T., 2012. The influence of host diversity and composition on epidemiological patterns at multiple spatial scales. Ecology 93, 1095–1105.
Moore, S.M., Manore, C.A., Bokil, V.A., Borer, E.T., Hosseini, P.R., 2011. Spatiotemporal model of Barley and Cereal yellow dwarf virus transmission dynamics with seasonality and plant competition. Bull. Math. Biol. 73, 2707–2730.
Morin, S., Ghanim, M., Zeidan, M., Czosnek, H., Verbeek, M., vandenHeuvel, J.F.J.M., 1999. A GroEL homologue from endosymbiotic bacter of the whitefly *Besmisia tabaci* is implicated in the circulative transmission of tomato yellow leaf curl virus. Virology 256, 75–84.
Nakatsukasa-Akune, M., Yamashita, K., Shimoda, Y., Uchiumi, T., Abe, M., Aoki, T., Kamizawa, A., Ayabe, S.-i., Higashi, S., Suzuki, A., 2005. Suppression of root nodule formation by artificial expression of the *TrEnodDR1* (coat protein of *White clover cryptic virus 2*) gene in *Lotus japonicus*. Mol. Plant–Microbe Interact. 18, 1069–1080.
Ng, T.F.F., Chen, L.-F., Zhou, Y., Shapiro, B., Stiller, M., Heintzman, P.D., Varsani, A., Kondov, N.O., Wong, W., Dent, X., Andrews, T.D., Moorman, B.J., Meulendyk, T., MacKay, G., Gilbertson, R.L., Delwart, E., 2014. Preservation of viral genomes in 700-y-old caribou feces from a subarctic ice patch. Proc. Natl. Acad. Sci. U. S. A. 111, 16842–16847.
Noda, H., Nakashima, N., 1995. Non-pathogenic reoviruses of leafhoppers and planthoppers. Semin. Virol. 6, 109–116.
Noreen, F., Akbergenov, R., Hohn, T., Richert-Pöggeler, K.R., 2007. Distinct expression of endogenous *Petunia vein clearing virus* and the DNA transposon dTph1 in two *Petunia hybrida* lines is correlated with differences in histone modification and siRNA production. Plant J. 50, 219–229.
Palukaitis, P., Roossinck, M.J., Dietzgen, R.G., Francki, R.I.B., 1992. Cucumber mosaic virus. In: Maramorosch, K., Murphy, F.A., Shatkin, A.J. (Eds.), Advances in Virus Research. Academic Press, San Diego, California, pp. 281–348.
Pan, H., Chu, D., Liu, B., Shi, X., Guo, L., Xie, W., Carrière, Y., Li, X., Zhang, Y., 2013. Differential effects of an exotic plant virus on its two closely related vectors. Sci. Rep. 3, 2230.
Phan, T.G., Kapusinszky, B., Wang, C., Rose, R.K., Lipton, H.L., Delwart, E.L., 2011. The fecal viral flora of wild rodents. PLoS Pathog. 7, e102218.
Power, A.G., Borer, E.T., Hosseini, P., Mitchell, C.E., Seabloom, E.W., 2011. The community ecology of *barley/cereal yellow dwarf viruses* in Western US grasslands. Virus Res. 159, 95–100.
Prendeville, H.R., Tenhumberg, B., Pilson, D., 2014. Effects of virus on plant fecudnity and populations dynamics. New Phytol. 202, 1346–1356.
Rajabaskar, D., Bosque-Pérez, N.A., Eigenbrode, S.D., 2014. Preference by a virus vector for infected plants is reversed after virus acquisition. Virus Res. 186, 32–37.
Rajabaskar, D., Wu, Y., Bosque-Pérez, N.A., Eigenbrode, S.D., 2013. Dynamics of *Myzus persicae* arrestment by volatiles from *Potato leafroll virus*-infected potato plants during disease progression. Entomol. Exp. Appl. 148, 172–181.
Rodelo-Urrego, M., Pagán, I., González-Jara, P., Betancourt, M., Moreno-Letelier, A., Ayllón, M.A., Fraile, A., Piñero, D., García-Arenal, F., 2013. Landscape heterogeneity shapes host–parasite interactions and results in apparent plant–virus co-divergence. Mol. Ecol. 22, 2325–2340.
Roossinck, M.J., 2010. Lifestyles of plant viruses. Philos. Trans. R. Soc. B 365, 1899–1905.
Roossinck, M.J., 2011. The good viruses: viral mutualistic symbioses. Nat. Rev. Microbiol. 9, 99–108.
Roossinck, M.J., 2012a. Persistent plant viruses: molecular hitchhikers or epigenetic elements?. In: Witzany, G. (Ed.), Viruses: Essential Agents of Life. Springer, Dordrecht, pp. 177–186.
Roossinck, M.J., 2012b. Plant virus metagenomics: biodiversity and ecology. Ann. Rev. Genet. 46, 357–367.
Roossinck, M.J., 2013. Plant virus ecology. PLoS Pathog. 9, e1003304.
Roossinck, M.J., 2014. Metagenomics of plant and fungal viruses reveals an abundance of persistent lifestyles. Front. Microbiol. 5, 767.
Roossinck, M.J., García-Arenal, F., 2015. Ecosystem simplification, biodiversity loss and plant virus emergence. Curr. Opin. Virol. 10, 56–62.
Roossinck, M.J., Martin, D.P., Roumagnac, P., 2015. Plant virus metagenomics: advances in virus discovery. Phytopathology, in press.
Roossinck, M.J., Sabanadzovic, S., Okada, R., Valverde, R.A., 2011. The remarkable evoluntionary history of endornaviruses. J. Gen. Virol. 92, 2674–2678.
Rosario, K., Nilsson, C., Lim, Y.W., Ruan, Y., Breitbart, M., 2009. Metagenomic analysis of viruses in reclaimed water. Environ. Microbiol. 11, 2806–2820.
Rúa, M.A., Pollina, E.C., Power, A.G., Mitchell, C.E., 2011. The role of viruses in biological invastions: friend or foe? Curr. Opin. Virol. 1, 68–72.
Ryabov, E.V., Keane, G., Naish, N., Evered, C., Winstanley, D., 2009. Densovirus induces winged morphs in asexual clones of the rosy apple aphid, *Dysaphis plantaginea*. Proc. Natl. Acad. Sci. U. S. A. 106, 8465–8470.
Salvaudon, L., DeMoraes, C.M., Mescher, M.C., 2013. Outcomes of co-infection by two potyviruses: implicatins for the evolution of manipulative strategies. Proc. R. Soc. B 280, 20122959.
Schrotenboer, A.C., Allen, M.S., Malmstrom, C.M., 2011. Modification of native grasses for biofuel production may increase virus susceptibility. GCB Bioenergy 3, 360–374.
Seabloom, E.W., Borer, E.T., Mitchell, C.E., Power, A.G., 2010. Viral diversity and prevalence gradients in North American Pacific coast grasslands. Ecology 91, 721–732.
Shapiro, L., DeMoraes, C.M., Stephenson, A.G., Mescher, M.C., 2012. Pathogen effects on vegetative and floral odours mediate vector attraction and host exposure in a complex pathosystem. Ecol. Lett. 15, 1431–1438.
Shapiro, L.R., Salvaudon, L., Mauck, K.E., Pulido, H., DeMoraes, C.M., Stephenson, A.G., Mescher, M.C., 2013. Disease interactions in a shared host plant: effects of pre-existing viral infection on Cucurit plant defense responses and resistance to bacterial wilt disease. PLoS One 8, e77393.
Stafford, C.A., Walker, G.P., Ullman, D.E., 2011. Infection with a plant virus modifies vector feeding behavior. Proc. Natl. Acad. Sci. U. S. A. 108, 9350–9355.
Staginnus, C., Gregor, W., Mette, M.F., Teo, C.H., Borroto-Fernández, E.G., Machado, M.L.D.C., Matzke, M., Schwarzacher, T., 2007. Endogenous pararetroviral sequences in tomato (*Solanum lycopersicum*) and related species. BMC Plant Biol. 7, 24.
Stobbe, A.H., Roossinck, M.J., 2014. Plant virus metagenomics: what we know and why we need to know more. Front. Plant Sci. 5, 150.
Su, Q., Pan, H., Liu, B., Chu, D., Xie, W., Wi, Q., Wang, S., Xu, B., Zhang, Y., 2013. Insect symbiont facilitates vector acquisition, retention, and transmission of plant virus. Sci. Rep. 3, 1367.
Tack, A.J.M., Dicke, M., 2013. Plant pathogens structure arthropod communities across multiple spatial and temporal scales. Funct. Ecol. 27, 633–645.
Tamaki, H., Zhang, R., Angly, F.E., Nakamura, S., Hong, P.-Y., Yasunaga, T., Kamagata, Y., Liu, W.-T., 2012. Metagenomic analysis of DNA viruses in a wastewater treatment plant in tropical climate. Environ. Microbiol. 14, 441–452.
vandenHeuvel, J.F.J.M., Verbeek, M., vanderWilk, F., 1994. Endosymbiotic bacteria associated with circulative transmission of potato leafroll virus by *Myzus persicae*. J. Gen. Virol. 75, 2539–2565.
vanderWant, J.P.H., Dijkstra, J., 2006. A history of plant virology. Arch. Virol. 151, 1467–1498.
vanMolken, T., deCaluwe, H., Hordijk, C.A., Leon-Reyes, A., Snoeren, T.A.L., vanDam, N.M., Stuefer, J.F., 2012. Virus infection decreases the attractiveness of white clover plants for a non-vectoring herbivore. Oecologia 170, 433–444.
vanMölken, T., Stuefer, J., 2011. The potential of plant viruses to promote genotypic diversity via genotype X environment interactions. Ann. Bot. 107, 1391–1397.
Victoria, J.G., Kapoor, A., Li, L., Blinkova, O., Slikas, B., Want, C., Naeem, A., Zaidi, S., Delwart, E., 2009. Metagenomic analysis of viruses in stool samples from children with acute flaccid paralysis. J. Virol. 83, 4642–4651.
Villarreal, L., Ryan, F., 2011. Viruses in host evolution: general principles and future extrapolations. Curr. Top. Virol. 9, 79–90.
Villarreal, L.P., 2005. Viruses and the Evolution of Life. ASM Press, Washington, DC.
Villarreal, L.P., Witzany, G., 2010. VIruses are essential agents within the roots and stems of the tree of life. J. Theor. Biol. 262, 698–710.
Virgin, H.W., 2014. The virome in mammalian physiology and disease. Cell 157, 142–150.
Wu, Y., Davis, T.S., Eigenbrode, S.D., 2014. Aphid behavioral responses to virus-infected plants are similar despiet divergent fitness effects. Entol. Exp. Appl. 153, 246–255.
Xu, P., Chen, F., Mannas, J.P., Feldman, T., Sumner, L.W., Roossinck, M.J., 2008. Virus infection improves drought tolerance. New Phytol. 180, 911–921.
Zhang, T., Breitbart, M., Lee, W.H., Rn, J.-Q., Wei, C.L., Soh, S.W.L., Hibberd, M.L., Liu, E.T., Rohwer, F., Ruan, Y., 2006. RNA viral community in human feces: prevalance of plant pathogenic viruses. PLoS Biol. 4 (e3), 1–8.
Zhang, T., Luan, J.-B., Qi, J.-F., Huang, C.-J., Li, M., Zhou, X.-P., Liu, S.-S., 2012. Begomovirus-whitefly mutualism is achieved through repression of plant defences by a virus pathogenicity factor. Mol. Ecol. 21, 1294–1304.