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Opinion piece

A new look at plant viruses and their potential beneficial roles in crops

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INTRODUCTION

Twenty years ago most people (including many scientists) thought of bacteria solely as agents of disease, best treated with disinfectants and antibiotics. Today, most of us are aware that bacteria make up almost 90% of the cells in our bodies, and play a critical role in digestion and the immune response. In plants, bacteria also form important mutualistic relationships, providing nitrogen fixation, growth enhancement and defence against pathogens, and undoubtedly a host of other functions that have yet to be described. The stigma of bacteria has changed dramatically in recent decades, and most people are aware that we need our good microbes.

Although there have been recent efforts to characterize the plant microbiome with a focus on finding beneficial microbes, viruses generally have not been included in the beneficial microbe lists (Berg *et al*., 2014, and references cited therein). Recent work has indicated that they can also play important and beneficial roles in plants, especially in extreme environments in which they are involved in conferring tolerance to drought, cold and hot soil temperatures (Roossinck, 2011). Beneficial viruses are defined for the purposes of this discussion as viruses that provide a trait to crop plants that increases their value or growth potential, or decreases the need for the use of chemical fertilizers or pesticides.

BENEFICIAL VIRUSES IN CROPS

Some of the best characterized beneficial viruses that have been used in plants are those that enhance the beauty of ornamental plants. *Tulip breaking virus* was the first of a long list of the beautiful viruses, but many other prized ornamentals owe their value, at least in part, to the viruses that infect them (Valverde *et al*., 2012). Other examples of beneficial plant viruses include several acute viruses (*Brome mosaic virus*, family *Bromoviridae*, *Cucumber mosaic virus*, family *Bromoviridae*, *Tobacco rattle virus*, family *Virgaviridae*, and *Tobacco mosaic virus*, family *Virgaviridae*), which confer tolerance to drought and freezing temperatures in several different crops, and persistent viruses, such as *White clover cryptic virus* (family *Partitiviridae*), which can suppress nodulation in legumes when adequate nitrogen is present (Roossinck, 2011). Plant virus strains with mild symptoms have been used for cross-protection against more severe strains, and this phenomenon has been exploited in pathogen-derived transgenic resistance strategies. In some cases, endogenous pararetroviruses can also protect against related viruses, but this is not always so (Roossinck, 2011). Are these just oddities? Or are we just overwhelmingly biased by our notions of viruses as pathogens?

Studies on virus biodiversity are indicating that plants are infected with numerous viruses that do not have any apparent ill effects on their hosts (Roossinck, 2012b). The persistent plant viruses, in the families *Chrysoviridae*, *Endornaviridae*, *Partitiviridae* and *Totiviridae*, are the most common viruses found in wild plants. These viruses have very long relationships with their plant hosts, being vertically transmitted for perhaps thousands of years, strongly implying a positive interaction. Persistent viruses are also common in crops, including peppers, rice, beans, carrots, figs, radish, white clover, melons, barley and avocados (Roossinck, 2012a). In some plants, sequences of persistent plant viruses are found in the genomes (Chiba *et al*., 2011; Liu *et al*., 2010), and these are often expressed. Interestingly, none of the plants reported to contain integrated sequences have cytoplasmic infections. Currently, the examples are too few to be conclusive, but this presents an intriguing hypothesis: if the persistent viruses are providing an important beneficial function for the plant, integration of the viral sequences into the genome would remove the need for a cytoplasmic version of the virus. It may be hard to fully decipher the potential of persistent virus functions in crop plants without looking to the origins of these plants. Environmental and nutritional conditions in crops are very different from in the native environment of their ancestral counterparts, where the persistent viruses presumably originally infected them, and where these long-term relationships evolved.

VIRUS–FUNGUS–PLANT INTERACTIONS

Endophytic fungi confer many well-recognized benefits to crops, although they have not been exploited to their potential. Fungi, in general, are very frequently infected with viruses, and endophytic fungi are no exception. *Curvularia thermal tolerance virus* is required for the thermotolerance of the plant–fungus–virus holobiont that allows a panic grass to grow in geothermal soils in

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Yellowstone National Park (Márquez *et al*., 2007). Although there are other examples of virus–fungus–plant interactions, they have not been studied, and the role of viruses in these systems has been largely ignored (Bao and Roossinck, 2013). However, it seems quite plausible that adding the right virus to an endophytic fungus could enhance its potential to provide further beneficial functions.

The discovery of *Cryphonectria hypovirus 1*, which attenuates the pathology of the causative agent of chestnut blight, sparked an interest in the use of viruses as biocontrol agents for plant pathogens. Viruses of plant-pathogenic fungi have been studied for their potential hypovirulence phenotypes, but few have been exploited for these purposes. Although there are technical challenges, for example the amount of variation in strains of the chestnut blight fungus in the USA has prevented the spread of the virus among isolates in natural environments (Dawe and Nuss, 2013), there are probably many additional examples of hypovirulence that have not been explored.

BACTERIAL VIRUSES

Unlike plant and fungal viruses, bacterial viruses often lyse their host cells after they multiply. Could these lytic viruses be exploited in agriculture? The use of phage therapy, i.e. using bacterial viruses to combat bacterial pathogens, has been explored for decades in humans and livestock, but has not been applied to plant pathology, where it seems that it would encounter far fewer obstacles of public perception than it has in humans. There has been experimental work in using phage against food-borne bacteria in crops, and the most common food-borne bacteria can be infected by many different phage, indicating the feasibility of this approach in plants. Lytic viruses of plant-pathogenic bacteria can be found in abundance in nature, and this approach has been attempted in a number of common bacterial diseases, including black rot in cabbage, citrus canker and fireblight, to name a few (Balogh *et al*., 2010). There are some complications to this approach, perhaps most significant being the diversity of bacteria and the specificity of phage. However, phage therapy would provide a very safe, non-toxic approach to combating pathogens, which would probably be more effective than current strategies, and deserves further exploration.

VIRUSES AFFECTING INSECT BEHAVIOUR

Viruses affecting the behaviour of insects have been described for many decades. Recent studies on plant–virus–insect interactions have shown that these relationships are old and complex. Virus infection can induce the release of volatiles from the plant to attract vectors to infected plants. Once a vector is feeding on the plant, the virus may induce antifeeding compounds to encourage the vector to move off to a new plant. The virus also seems to be able to manipulate the insect to prefer uninfected plants (Ingwell *et al*., 2012; Mauck *et al*., 2012). Could viruses also attract beneficial insects, such as pollinators, to crop plants? Viruses can also affect herbivorous insects in a negative way. Whiteflies feeding on plants infected with *Tomato spotted wilt virus* have slower development and reduced fecundity (Pan *et al*., 2013). These studies again illustrate how little we know about the complex ecology of viruses. Could we exploit these effects of viruses to help control damaging insects in crops?

CONCLUSIONS

The genomics era is revealing a whole new way of looking at life: most of the eukaryotic genomes are NOT protein coding sequences, yet much is still transcribed; genomes are riddled with viruses from the past, with estimates for the viral origin of genomes at 50% or greater; and wild plants are filled with RNAs that do not have any cognizant sequences in any databases. In virus biodiversity studies of wild plants, about 60% of all the sequences are orphans. It seems highly unlikely that these are just unknown genes in wild plants, whose genome sequences have not been determined, especially as they can also be found in crop plants (M. J. Roossinck, unpublished data).

Viruses have a great deal of potential for the benefit of agriculture, but this will require that we let go of our almost ubiquitous bias about the negative nature of viruses. Beneficial effects have been very poorly studied, and unexploited in crops. With our changing environment and the increase in extreme weather conditions, lack of adequate water and loss of arable lands, which are concurrent with ever-increasing human populations, we need to make use of every possible tool at our disposal to enhance agricultural production without further compromising the environment. Viruses hold the potential for safe, inexpensive and non-destructive improvements to cropping practices that need to be taken seriously by horticulturists, crop scientists and plant pathologists.

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REFERENCES

Balogh, B., **Jones, J.B.**, **Iriarte, F.B. and Momol, M.T.** (2010) Phage therapy for plant disease control. *Curr. Pharm. Biotechnol*. **11**, 48–57.

Bao, X. and Roossinck, M.J. (2013) Multiplexed interactions: viruses of endophytic fungi. In: *Fungal Viruses* (Ghabrial, S., ed.), pp. 37–57. San Diego: Elsevier.

Berg, G., **Grube, M.**, **Schloter, M. and Smalla, K.** (2014) Unraveling the plant microbiome: looking back and future perspectives. *Front. Microbiol*. **5**, 48.

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

Dawe, A.L. and Nuss, D.L. (2013) Hypovirus molecular biology: from Koch's postulates to host self-recognition genes that restrict virus transmission. *Adv. Virus Res.* **86**, 110–147.

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

Liu, H., **Fu, Y.**, **Jiang, D.**, **Li, G.**, **Xie, J.**, **Cheng, J.**, **Pend, Y.**, **Ghabriel, S.A. and Yi, X.** (2010) Widespread horizontal gene transfer from double-stranded RNA viruses to eukaryotic nuclear genomes. *J. Virol*. **84**, 11 879–11 887.

Márquez, L.M., **Redman, R.S.**, **Rodriguez, R.J. and Roossinck, M.J.** (2007) A virus in a fungus in a plant—three way symbiosis required for thermal tolerance. *Science*, **315**, 513–515.

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

Pan, H., **Chen, G.**, **Li, F.**, **Wi, Q.**, **Want, S.**, **Xie, W.**, **Liu, B.**, **Xu, B. and Zhang, Y.** (2013) Tomato spotted wilt virus infection reduces the fitness of a nonvector herbivore on pepper. *J*. *Econom*. *Entomol*. **106**, 924–928.

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: *Viruses: Essential Agents of Life* (Witzany, G., ed.), pp. 177–186. Dordrecht: Springer.

Roossinck, M.J. (2012b) Plant virus metagenomics: biodiversity and ecology. *Annu*. *Rev*. *Genet*. **46**, 357–367.

Valverde, R.A., **Sabanadzovic, S. and Hammond, J.** (2012) Viruses that enhance the aesthetics of some ornamental plants: beauty or beast? *Plant Dis*. **98**, 600–611.