Chapter 9
Symbiosis, Mutualism and Symbiogenesis

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Abstract Symbiosis is defined as two or more dissimilar entities living in or on one another in an intimate relationship. This definition encompasses both virus–virus and virus–host relationships. Symbiosis can be manifest as different lifestyles, from antagonistic (i.e., pathogenic) to mutualistic. Virus–virus and virus–host symbioses also manifest these different lifestyles, although the antagonistic lifestyles for virus–host relationships are the ones most studied, and hence most familiar. Studying viruses from the viewpoint of symbiosis emphasizes the relationships rather than the individuals in the partnerships. Symbiotic relationships can lead to the fusion of the entities, resulting in the formation of a new species, a process known as symbiogenesis. Plant viruses clearly have undergone repeated symbiogenesis in the evolution of the extant species, as evidenced by phylogenetic analyses, as well as a number of examples of viruses in the process of speciation.

9.1 Introduction

Symbiosis, as the term was originally coined by Frank and de Bary, requires two or more dissimilar entities living in or on one another in intimate contact (de Bary 1879). Symbiosis does not require mutualism, where both entities benefit from the relationship, which is only one of the potential lifestyles of a symbiotic relationship. Symbionts also can be commensal, where partners neither benefit nor are

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harmed, or antagonistic, where one or more partners benefit at the expense of the other(s). Historically viruses have not been described in terms of symbiosis, but recently this concept has gained acceptance (Margulis et al. 2007; Ryan 2007; Villarreal 2007). For the most part, viruses have been considered only as antagonists of their hosts, and are generally described as pathogens.

For plant viruses, almost all of the literature to date describes pathogenic viruses of crop plants. Studies on the occurrence and biological effects of plant viruses in wild hosts are beginning to surface only now (Wren et al. 2006). Here I will discuss two aspects of plant viral symbiosis: symbiotic relationships with host plants; and virus–virus symbiosis in mixed infections. In both types of relationships symbiosis can lead to symbiogenesis, the generation of a novel species by fusion of two species (Ryan 2006).

9.2 Virus–Host Symbiosis

Viruses are obligate intracellular parasites, requiring host machinery for most of their biological processes. Plant viruses (excluding the algal viruses) are relatively small in genomic content, probably because a small virion is necessary for their systemic spread, and hence require more from their hosts than some of the large animal or bacterial viruses, which can have genomes larger than some bacteria (Raoult et al. 2004). The relationship between plant viruses and their hosts is, for the most part, thought to be antagonistic, but that is likely because they have been studied only in terms of disease. There are a growing number of viruses found in plants that could be classified as persistent and commensal. Cryptic viruses have been known for some time (Boccardo et al. 1987), and more recently endornaviruses (endogenous RNA viruses), a group of large double-stranded RNA viruses have been described from numerous plants (Fukuhara et al. 2006). These viruses apparently are not transmitted from plant to plant, but are passed from generation to generation through seed. Interestingly, they have relatives in the fungal viruses (Boccardo and Candresse 2005; Hacker et al. 2005), and it seems possible that they originated as fungal viruses that became trapped in plants during a plant–fungus endophytic interaction (Roossinck 1997). No phenotype has been ascribed to the presence of these viruses, but since it is difficult to cure plants of them, they may express a subtle phenotype that is not apparent. Totiviruses, another family of fungal viruses, may also infect plants (Martin et al. 2006). Mutualistic viruses have not been described in plants, but they clearly are found in animal and insect virus systems (Rossignol et al. 1985; Webb 1998; Turnbull and Webb 2002; Moran et al. 2005; Stasiak et al. 2005). Viruses are also involved in more complex symbiotic relationships that involve plants. The mutualistic endophytic fungus *Curvularia protuberata* requires a virus to confer thermal tolerance to plants (Márquez et al. 2007). Plant viruses can also provide a benefit for their insect vectors (Belliure et al. 2005). When the field of plant virology overcomes the bias for pathogenic viruses of crop plants it is likely that many more examples will be found.

It is useful to think of viruses in terms of symbionts rather than to think of plants and viruses as independent entities, because this focuses on the interactions. Although experimental studies usually strive to bring everything to its simplest form, in nature all life exists in highly interactive and interdependent communities (see Chap. 2).

9.3 Virus–Host Symbiogenesis

Symbiogenesis was first recognized as an alternative model for evolution in the early twentieth century (Carrapiço and Rodrigues 2005). The evolution of the eukaryotic cell clearly involved symbiogenic events in the incorporation of organelles, but virus–host symbiogenesis may be much more important than previously recognized. Footprints of viral genes are found throughout most genomes that have been sequenced, including those of plants (Mette et al. 2002; Staginnus and Richert-Pöggeler 2006; also see Chap. 4), and viruses have probably played important roles in the evolution of their hosts, including the development of flowering plants (reviewed in Villarreal 2005). While reports of viruses in vascular plants are abundant, especially viruses inducing acute infections, reports of viruses in primitive plants such as mosses and liverworts are lacking. One example exists of viruses found in hornworts, and these are related to viruses from crop plants (Okuno et al. 2003). The deficiency may be due to the lack of looking rather than a true absence of viruses in these plants, but if acute disease-causing infections were common in primitive plants it is likely that they would have been noticed. The evolution of vascular plants coincides with a huge expansion in genome size, and this could be due to massive colonization by genetic parasites, including viruses. The evolution of angiosperms (flowering plants) represents an explosion of new species, and coincidently, the number of viruses that can infect flowering plants is vastly larger than for other plants (Villarreal 2005). It is an intriguing possibility that the two are linked.

Virus–host symbiogenesis can also result in virus speciation through the acquisition of new genes from the host by the virus. This has been documented in at least one case (Mayo and Jolly 1991), and has been seen in experimental evolution studies involving virus infections of transgenic plants (Allison et al. 1990, 1996). The movement proteins of plant viruses may have been acquired from their hosts, as these proteins show an extraordinary level of diversity in viruses whose replicase genes are closely related (Melcher 2000), and plants express proteins that are functionally very similar to plant virus movement proteins (Lucas et al. 1995; Xoconostle-Cázares et al. 1999).

9.4 Virus–Virus Symbiosis

Mixed infections of plant viruses are common and well documented. To be considered symbiotic, however, there must be evidence of interaction. Plant virus synergy, first described in the 1950s (Rochow and Ross 1955), is a well-known example of plant virus symbiosis. In synergy, the disease symptoms are enhanced by the mixed infection. The most well documented examples of synergy involve potyviruses, and result in enhanced replication of the partner virus, while the potyvirus replication is not affected (Vance 1991; Pruss et al. 1997). At least in some cases this was shown to involve suppression of post-transcriptional gene silencing by the potyvirus (Anandalakshmi et al. 1998). Synergy occurs among DNA viruses as well as RNA viruses of plants, and has been documented for the geminiviruses (Fondong et al. 2000; Pita et al. 2001), and between an RNA virus and a DNA virus (Hii et al. 2002). Synergy can result in enhanced replication of one, both or neither partner (reviewed in Zhang et al. 2001).

Support of satellite RNAs or viruses is another form of symbiosis that is found in plant viruses. The helper virus is responsible for replication and dissemination of the satellite element. Strictly defined, satellites do not provide any essential functions for the helper virus, but they can alter the symptom phenotype by either attenuating or exacerbating symptoms (Xu and Roossinck 2001; Simon et al. 2004). In general, these elements have an antagonistic affect on the replication of the helper virus.

A number of plant viruses exhibit another form of symbiosis called interdependence. These symbiotic interactions are often obligate. They can be required for vector transmission, as in the umbravirus/luteovirus symbioses (Gibbs 1995) and the rice tungro disease viruses (Hull 2002), or in establishment of systemic infection, as with *Pepper veinal mottle virus* and *Potato virus Y* (Marchoux et al. 1993) and other potyvirus combinations, or with *Pepper mottle virus* and *Cucumber mosaic virus* (CMV; Guerini and Murphy 1999).

9.5 Virus–Virus Symbiogenesis

The role of symbiogenesis in the evolution of RNA viruses of plants has been reviewed recently (Roossinck 2005). When symbiotic viruses exchange genomic elements a new viral species is formed. The results of these symbiogenic events are usually seen in phylogenetic analyses, where different portions of the viral genomes yield trees that are not congruent (Morozov et al. 1989; Roossinck 2002; Morozov and Solovyev 2003). This has been termed “modular evolution” (Botstein 1980). The modular nature of plant virus proteins means that viruses in symbiotic relationships in mixed infections have been frequently reassorted and recombined to form new species. This gives plant viruses an enormous level of flexibility and a capacity for very rapid evolutionary changes. A number of recently described examples of new RNA virus species likely formed through symbiogenesis include *Poinsettia latent virus*, which appears be a recombinant between a polerovirus and a sobemovirus (aus dem Siepen et al. 2005); *Bean leafroll virus* and *Sugarcane yellow leaf virus*, the products of recombination events between luteo-like and polero-like viruses (Moonan et al. 2000; Domier et al. 2002); and *Bean distortion mosaic virus*, the result of both reassortment and recombination between *Peanut stunt virus* and

CMV (White et al. 1995; Roossinck, unpublished data); and the tobravirus strains I6 and N5, which resulted from the reassortment of elements from *Tobacco rattle virus* and *Pea early browning virus* (Robinson et al. 1987). Experimental evolution has also yielded new symbiogenic viruses that are the result of recombination between *Tomato aspermy virus* and CMV (Aaziz and Tepfer 1999; de Wispelaere et al. 2005).

Symbiogenesis also has been involved in the evolution of plant DNA viruses. A great deal of the emergence of new geminiviruses has been attributed to reassortment and recombination (Rojas et al. 2005; Seal et al. 2006; also see Chap. 3). Reassortment has probably been important in the evolution of the extant *Banana bunchy top virus* group as well (Hu et al. 2007). Even viroids have not escaped the role of symbiogenesis in their evolution, and recent analyses of numerous *Peach latent mosaic viroid* isolates show clear evidence of recombination (Hassen et al. 2007).

9.6 Conclusions

Considering virus–virus and virus–host interactions in terms of symbiosis and symbiogenesis provides a framework to emphasize the interactions that shape evolution. For the most part, only the antagonistic relationships in virus–host symbioses have been explored, while more mutualistic relationships have been described for virus–virus interactions. Symbiotic and symbiogenic interactions, which affect the evolution of all life on earth, are only beginning to be studied. Theoretical frameworks are still being developed. Viruses, which can adapt rapidly to new environments, provide an ideal experimental system for understanding the complex interactions in communities of life, the way life exists in nature.

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