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Review

Synergies and antagonisms in virus interactions

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ABSTRACT

Metagenomic surveys and data from next generation sequencing revealed that mixed infections among plant viruses are probably a rule rather than an exception in natural pathosystems. The documented cases may range from synergism to antagonism, which may depend from the spatiotemporal order of arrival of the viruses on the host and upon the host itself. In synergistic interactions, the measurable differences in replication, phenotypic and cytopathological changes, cellular tropism, within host movement, and transmission rate of one of the two viruses or both are increased. Conversely, a decrease in replication, or inhibition of one or more of the above functions by one virus against the other, leads to an antagonistic interaction. Viruses may interact directly and by transcomplementation of defective functions or indirectly, through responses mediated by the host like the defense mechanism based on RNA silencing. Outcomes of these interactions can be applied to the risk assessment of transgenic crops expressing viral proteins, or cross-protected crops for the identification of potential hazards. Prior to experimental evidence, mathematical models may help in forecasting challenges deriving from the great variety of pathways of synergistic and antagonistic interactions. Actually, it seems that such predictions do not receive sufficient credit in the framework of agriculture.

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1. Introduction

"We don't know how much we're missing right now but we know that every time we change techniques we find new viruses" [1] .

New sequencing technologies and metagenomic surveys have changed the way we consider the etiology of viral diseases in plants. Most of the attention has been given to individual virus species and strains as unique or principal agents of disease whereas multiple infections, interactions between viruses or between viruses and other (micro)organisms have received less attention.

The latest discoveries in plant virology have contributed to a more comprehensive understanding of the plant virome, which includes the collection of viruses that infect host cells, the virus-derived sequences embedded in host genome and the viruses that interact with or infect broad arrays of other types of eukaryotic and prokaryotic organisms inhabiting the same host [2]. Virome sequencing from symptomatic and asymptomatic plants provides a census of the viral population in wild, ornamental, and crop communities, suggesting that multiple infections involving two or more known and unknown viruses are more common than expected. They are probably the rule rather than an exception in natural pathosystems. The effects of such mixed infections are unpredictable and may range from lethal to beneficial. This, in turn, has provided the basic knowledge for modern approaches to resolve the unknown etiology of some diseases and to propose new strategies for controlling viruses [3,4].

Interactions of viruses in mixed infections before the metagenomic era was generally studied by laboratory experiments reproducing real cases discovered accidentally in the field. The viruses found using metagenomic sequencing can be clustered in three levels of knowledge [5,6]: i) virus species or strains that are already known to be present in the area/host surveyed; ii) new virus species or strains of known viruses that have not been found previously in the area/host surveyed; iii) viruses that are completely novel.

In studying on how viruses interact with each other in a plant virome, one may consider only viral species [7], or viral species together with other eukaryotic and prokaryotic micro(organisms) [8], and whether the virus-virus interaction is direct or mediated by host functions [8,9]. This requires a key preliminary decision as removal of non-viral sequences before or after sequencing or enrichment of the sample for plant virus specific sequences, like double-stranded RNAs or small interfering RNAs (siRNA) would increase the probability to detect unknown viruses, but introduces obvious bias against other (micro)organisms.

The aim of this review is to describe and comment on selected examples of synergistic and antagonistic viral interactions in plants and highlight the great variety of their pathways (Fig. 1). Major points discussed are summarized at the end of each section.

2. Technical advances in the study of plant virome: next generation sequencing and metagenomic analysis

Compared to other biological systems or pathogens, the implementation of next generation sequencing (NGS) and metagenomic analysis in the study of plant virome is relatively recent because viruses do not contain conserved genomic regions such as ribosomal genes that can be used for their identification in a microbial community [2,10]. Alternative approaches have been proposed to overcome this problem [11,12] that have rapidly led to the simultaneous detection of both known and unknown viruses in a number of different hosts, including plants, without the necessity of any prior knowledge of the virus sequence [10,13,14].

A metagenomic approach, i.e. the genomic analysis of microbial communities, utilizes NGS to sequence the total nucleic acid content in a biological sample [15] and bioinformatic tools to identify specific pathogens from sequencing outputs. In this way the metagenomic analysis overcomes the biases introduced in the identification of individual viruses as etiological agents of disease in complex arrays of microbes.

2.1. Next generation sequencing platforms

Roche 454 GS-FLX, HiSeq 2000 Illumina and Applied Biosystems SOLiD^{TM} System (Life Technologies) are among the NGS platforms used more frequently but there are other platforms available and new ones are currently being developed to simplify sample preparation and to reduce costs and time for the analysis [reviewed in Refs. [16–19]]. The Roche 454, Illumina and SOLiD System utilize different biochemical approaches but basically all include a PCR step for the amplification of the libraries to be sequenced, a pause for nucleotide identification and detection methods to capture the light or fluorescence emitted by a reporter molecule after nucleotide incorporation.

Briefly, Roche 454 platform detects the light emitted by the pyrophosphate moiety released after incorporation of each nucleotide during DNA polymerization. This pyrophosphate catalyzes emission of visible light through a series of downstream reactions that require the activity of the enzymes sulfurylase and luciferase. The light emitted is proportional to the number of nucleotides incorporated, is captured by a high-resolution charge-coupled device (CCD) camera and converted into sequencing data. The average number of sequence data (reads) produced by the current 454 GS-FLX+ sequencer is more than 1 million of 700 bp reads within 23 h [19].

The HiSeq 2000 Illumina platform produces clusters of thousands of original sequences by a process called bridge amplification and sequences hundreds of millions of such clusters per run. Each nucleotide is coupled with a reversible chemically blocked dye terminator that blocks DNA chain elongation after incorporation, so that the signal emitted by the last base added is detected by a CCD camera and the corresponding nucleotide identified. After identification, the chemical block is removed allowing incorporation of the next fluorescent group. The new Illumina MiSeq platform generates up to 15 Gb of 2×300 bp reads in only 55 h [19].

The SOLiD system uses DNA ligase instead of DNA polymerase and sequences single-stranded DNA libraries immobilized on magnetic beads. The platform employs sets of semi-degenerate 8-mer oligo probes carrying four distinct fluorescent labels to scan the immobilized DNA. When an 8-mer oligo hybridizes to the complementary DNA sequence a ligation reaction occurs and the base incorporated is identified by the fluorescent label. A chemical cleavage between the fifth and sixth base of the hybridized oligo removes the fluorescent group allowing the next ligation round. The SOLiD 5500xl system currently generates 95 Gb of 2×60 bp reads during 6 days [19].

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