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The battle for survival between viruses and their host plants

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Evolution has equipped plants with defense mechanisms to counterattack virus infections. However, some viruses have acquired the capacity to escape these defense barriers. In their combats, plants use mechanisms such as antiviral RNA silencing that viruses fight against using silencing-repressors. Plants could also resist by mutating a host factor required by the virus to complete a particular step of its infectious cycle. Another successful mechanism of resistance is the hypersensitive response, where plants engineer R genes that recognize specifically their assailants. The recognition is followed by the triggering of a broad spectrum resistance. New understanding of such resistance mechanisms will probably helps to propose new means to enhance plant resistance against viruses.

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Introduction

Plants are constantly challenged by pathogens from all kingdoms like nematodes, fungi, bacteria and viruses. To defend themselves and prevent disease, plants have evolved sophisticated and efficient mechanisms. One of the most common disease defense is the induction of a rapid localized cell death at the point of pathogen infection, called hypersensitive response (HR). The HR can be triggered by a wide variety of pathogens, including viruses, and relies mainly on dominant resistance (R) genes, which recognize pathogen-derived effector proteins. In this short review, we intend to first, provide a brief overview of severe virus-associated plant diseases and their impact on crop production, second, to present the current state of knowledge on vectors for virus transmission, and third, to summarize recent progress in understanding plant resistance against viruses focusing on the R genes mediated dominant resistance.

Viruses and diseases

Viruses are obligate intracellular parasites absolutely dependent on the host cell machinery to multiply and spread. They are nucleic acid-based pathogens with genomes that consist of single-stranded or double-stranded RNAs or DNAs encoding few genes and usually packed into protein envelopes called the capsid. Viruses invade all forms of life and viral infection causes physiological disorders leading to diseases. Viral diseases are undoubtedly one of the most limiting factors that cause significant yield loss and continuously threaten crop production worldwide. Damages range from stunted growth, reduced vigor, decreased market esthetic values of the products and/or total yield loss. Although it's very complex to put a clear figure on the economic impact of plant diseases in agriculture, it was estimated that 15% of global crop production is lost due to pre-harvest plant disease [1] and viruses account for 47% of the plant diseases [2]. In South-East Asia, viruses such as the tungro viral disease (*Rice tungro spherical virus* and *Rice tungro bacilliform virus*), the *Rice yellow mottle virus* (RYMV) and the *Rice stripe virus* (RSV) were reported to cause yield losses of 50–100% estimated to an annual economic loss of more than US$1.5 billion [3••]. In East and Central Africa, the *African cassava mosaic virus* (ACMV), the major constraint for cassava cultivation, was reported to cause yield losses of 47% of the production corresponding to economic loss of more than US$2 billion [4].

Virus-transmitting vectors

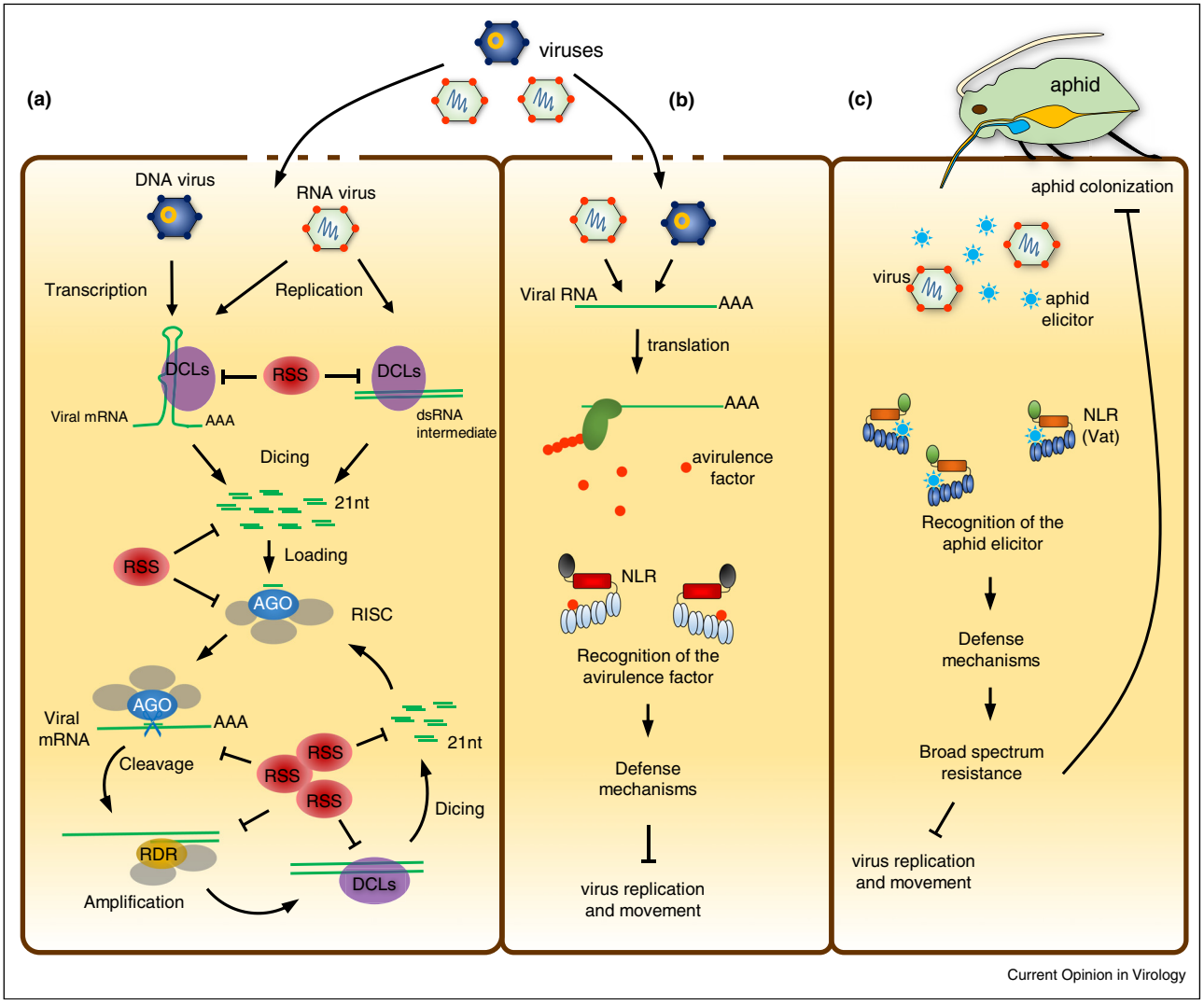
An important feature shared by plant viruses is their efficient movement from host to host. This virus transmission is a vital step in the biological cycle of viruses because it ensures their maintenance, survival and spread. The virus transmission cycle involves a continuum of processes, acquisition of the virus when the vector feeds on a virus-infected plant, stable retention and transport of the virus within the vector, and inoculation of the retained virus into a new host plant during a subsequent feeding. Most plant viruses (76%) are transmitted by a diverse array of vectors including insects, nematodes and fungi. Many of these vectors are plant pests, and their association with plants

makes them ideal agents for efficient local and long-distance virus spread. By far, insects, the most common plant virus vectors, transmit the majority of described plant viruses, and of these, hemipteran insects transmit 55% of the vectored viruses [5]. In most cases, viruses of a given taxon have a specific type of insect vector. For example, viruses of the genus *Potyvirus* and *Begomovirus* are solely transmitted by aphids and whiteflies, the most economically important insect vectors, respectively.

Antiviral RNA silencing defense

Once infected, plants rely on elaborate antiviral immune arsenal to defend themselves against the invading viruses. One of the immediate antiviral defense plant viruses encountered when invading a host is the RNA silencing (Figure 1a) [6]. RNA silencing, also called RNA interference (RNAi), is an evolutionary conserved and sequence-specific mechanism that directly defends host cells against foreign nucleic acids such as viruses and transposable elements [7]. This defense is triggered by double-stranded RNA molecules (dsRNA). Most plant viruses have RNA genomes that replicate through dsRNA intermediates by viral RNA-dependant RNA polymerases (RDRs) or contain double-stranded secondary structures. These viral dsRNAs are processed by Dicer-like (DCL) enzymes into virus-derived small RNAs (vsRNAs) that

Figure 1



Mechanisms of plant resistance to viruses. **(a)** Antiviral RNA silencing in plants and its suppression by virus-encoded RNA silencing suppressors (RSSs). RNA silencing is initiated by the recognition of viral dsRNAs or partially double strand hairpin RNAs, which are processed to vsiRNAs. (**b**) NLR-mediated plant resistance. Following entry into a host cell, viral effectors are expressed from the virus genome. Specific plant NLR genes interact (directly or indirectly) with these effectors to trigger virus resistance. (**c**) Model for *Vat*-mediated resistance involving separate recognition and response phases. In the *A. gossypii* resistant plant, the Vat-NLR recognizes an elicitor molecule from the aphid. This recognition phase induces local resistance mechanisms that inhibit aphid colonization and replication and movement of viruses transmitted by the same aphid.