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Current Opinion in Virology

Insect cuticular proteins and their role in transmission of phytoviruses

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Many viruses of agricultural importance are transmitted to host plants via insect vectors. Characterizing virus–vector interactions at the molecular level is essential if we are to fully understand the transmission mechanisms involved and develop new strategies to control viral spread. Hitherto, insect proteins involved in virus transmission have been characterized only poorly. Recent advances in this topic, however, have significantly filled this knowledge gap. Among the vector molecules identified, cuticular proteins have emerged as key molecules for plant virus transmission, regardless of transmission mode or vector considered. Here, we review recent evidence highlighting that the CPR family, and particularly RR-1 proteins, undoubtedly deserves special attention.

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Current Opinion in Virology 2018, **33**:137–143

This review comes from a themed issue on **Virus-vector interactions**

Edited by **Anna E Whitfield** and **Ralf Dietzgen**

https://doi.org/10.1016/j.coviro.2018.07.015

Introduction

To ensure sustainability in the environment, phytoviruses must overcome two major constraints: their hosts are immobile, and the plant cell wall represents a physical barrier that viruses have to cross before they can replicate and spread in plant tissues. Most plant viruses are transmitted horizontally and re-transported by plant-feeding organisms (vectors) that are able to move from plant to plant [1,2]. The most frequent vectors of plant viruses are hemipteran and thysanopteran insects with piercing-sucking mouthparts, including aphids, whiteflies, leafhoppers, planthoppers, and thrips [2]. Virus–vector interactions, which are sophisticated and highly specific [3], can be classified into two main categories (for a review see [4]). Noncirculative viruses are reversibly attached to the cuticle of the insect mouthparts, in the stylets or foregut of their vectors [4–6], during their journey from one plant to another. Circulative viruses are 'internalized' in the vector body, and must cross the gut barrier to reach the hemolymph and/or other tissues. Ultimately, viruses reach the salivary glands, and are injected, together with vector saliva, into new host plants. A few virus species have been shown to replicate within their vectors during their journey and have been classified in the circulative propagative subcategory [7]. Numerous studies have focused on elucidating the mechanisms underlying vector transmission [3,5,6,8], and viral determinants have been well characterized for most plant virus species studied. These include structural proteins, membrane viral glycoproteins, or non-structural virus-encoded proteins [4,9,10]. However, an extensive study of virus–vector interactions at the molecular level is still challenged by the difficulty of identifying vector partners and validating their role in virus transmission [11••,12••,13••,14••,15••].

Nonetheless, considerable efforts have been made to develop complementary approaches and high-throughput methods to help identify vector proteins involved in virus–vector interactions. Among these interacting molecules are several cuticular proteins (CuPs) [13••,15••,16,17,18••,19–26]. CuPs are chitin-binding proteins that contribute to cuticle structural integrity, and reflect its diversity and mechanical properties [27–29]. CuPs have been classified into 14 families [30•,31,32], the most abundant by far being the CPR family comprising proteins with a Rebers and Riddiford (RR) consensus [33]. The RR family is divided into three subfamilies, RR-1, RR-2, RR-3 [30•], to which most identified virus-interacting proteins can be assigned (Table 1). Their role as a key partner of both noncirculative and circulative plant viruses was hitherto unforeseen. Here, we review striking advances in the characterization of CuP–virus interactions that have brought novel insights to the field of vector transmission of plant viruses.

Role of cuticular proteins in noncirculative plant virus transmission

Noncirculative viruses bind reversibly to specific retention sites on the cuticle of the feeding apparatus. Therefore, virus-interacting molecules should be cuticular compounds that fulfill the role of virus receptors. To date, receptors of foregut-borne viruses have been poorly characterized [34,35], and no CuP has been shown to be involved in their retention or transmission. The great majority of noncirculative viruses, among which are members of the families *Potyviridae*, *Bromoviridae* and

Table 1

Cuticular proteins (CuPs) identified in the virus–insect vector interaction studies presented in this review

Virus species/genus	Vector — *species*	Transmission mode	CuPs identifier[a] — *other name*	Protein family[b] (subfamily)	Approaches	Reference
ZYMV/*Potyvirus*	Aphid — *M. persicae*	Noncirculative	AAO63549	CPR (RR-2)	Urea extraction of aphid CuPs, 1-D & 2-D gel electrophoresis, Far-western blot, MS analyses	[17]
			AAL29466	CPR (RR-2)		
			AAZ20451	CPR (RR-1)		
			AAZ20447	CPR (RR-2)		
CaMV/*Caulimovirus*	Aphid	Noncirculative	ND	ND	Biochemical characterization, Stylet immunolabeling	[40•]
CaMV/*Caulimovirus*	Aphid — *A. pisum, M. persicae*	Noncirculative	MG188739 — *Stylin-01*	CPR (RR-1)	Stylet immunolabeling, Colocalization, *in vitro* competition assays, RNAi	[15••]
			MG188741 — *Stylin-01*	CPR (RR-1)		
CMV/*Cucumovirus*	Aphid — *M. persicae*	Noncirculative	DQ108938 — *Mpcp4*	CPR (RR-1)	YTH	[22]
CMV/*Cucumovirus*	Aphid — *A. pisum*	Noncirculative	ND	CPR (RR-2)	Peptide array (RR-2 proteins)	[25]
TuYV[c]/*Polerovirus*	Aphid — *M. persicae*	Circulative	ND[d]	ND	Whole cell lysate (aphids), 1-D & 2-D gel electrophoresis, Far-western blot & MS analyses	[16]
CYDV-RPV/ *Polerovirus*	Aphid — *S. graminum*	Circulative	gi:193647865	CPR (RR-2)	Genetics coupled to 2-D-DIGE & MS analyses	[18••]
			gi:193706873	ND[d]		
			gi:193647875	CPR (RR-2)		
			gi:193582403	CPR (RR-2)		
BYDV-GPV/ *Luteoviridae*[e]	Aphid — *R. padi*	Circulative	gi:288558725 — *Cp 62 precursor*	CPR (RR-2)	iTRAQ & MS analyses	[20]
			NP_001156154.1 — *Cp 5 precursor*	CPR (RR-2)		
RSV/*Tenuivirus*	Planthopper — *L. striatellus*	Circulative-Propagative	KC485263 — *CPR1*	CPR (RR-1)	YTH, Chemiluminescent co-IP, Colocalization, GST pull-down, RNAi	[13••]
RSV/*Tenuivirus*	Planthopper — *L. striatellus*	Circulative-Propagative	XM_014390248.1 — *Cuticle protein A3A like*	CPR (RR-2)	YTH	[26]
			JAS02196.1	Tweedle		

[a] Given accession numbers from original studies.
[b] Classified using CutProtFam-Pred (http://aias.biol.uoa.gr/CutProtFam-Pred/).
[c] Formerly BWYV-FL1 (beet western yellows virus).
[d] published accession number does not correspond to a CuP according to databases and CutProtFam-Pred.
[e] Unassigned member in the family Luteoviridae. CuP: cuticular protein; ND: not determined; MS: mass spectrometry; RNAi: RNA interference; DIGE: difference gel electrophoresis; iTRAQ: isobaric tags for relative and absolute quantification; co-IP: co-immunoprecipitation; YTH: yeast two-hybrid. ZYMV: zucchini mosaic virus; CaMV: cauliflower mosaic virus; CMV: cucumber mosaic virus; TuYV: turnip yellows virus; CYDV: cereal yellow dwarf virus; BYDV: barley yellow dwarf virus, RSV: rice stripe virus.