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Viral receptors of the gut: insect-borne propagative plant viruses of agricultural importance

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Insect-borne propagative plant viruses of agricultural importance are transmitted by sap-sucking insects. Although the infection routes of these viruses within the bodies of insect vectors are well established, cellular receptors on the microvilli, intercellular junctions, and basal lamina for mediating viral entry or spread in insect gut epithelium have not been well identified or characterized. Recent trends in the field are opening questions on how viruses exploit actin-based tubule motility to overcome insect gut epithelium barriers after viral entry in epithelium. Advances in insect cell lines, genome sequencing, reverse genetic systems and others not yet developed technologies are needed to find and characterize the counterpart receptors in vectors and to design strategies to interfere with viral transmission.

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Introduction

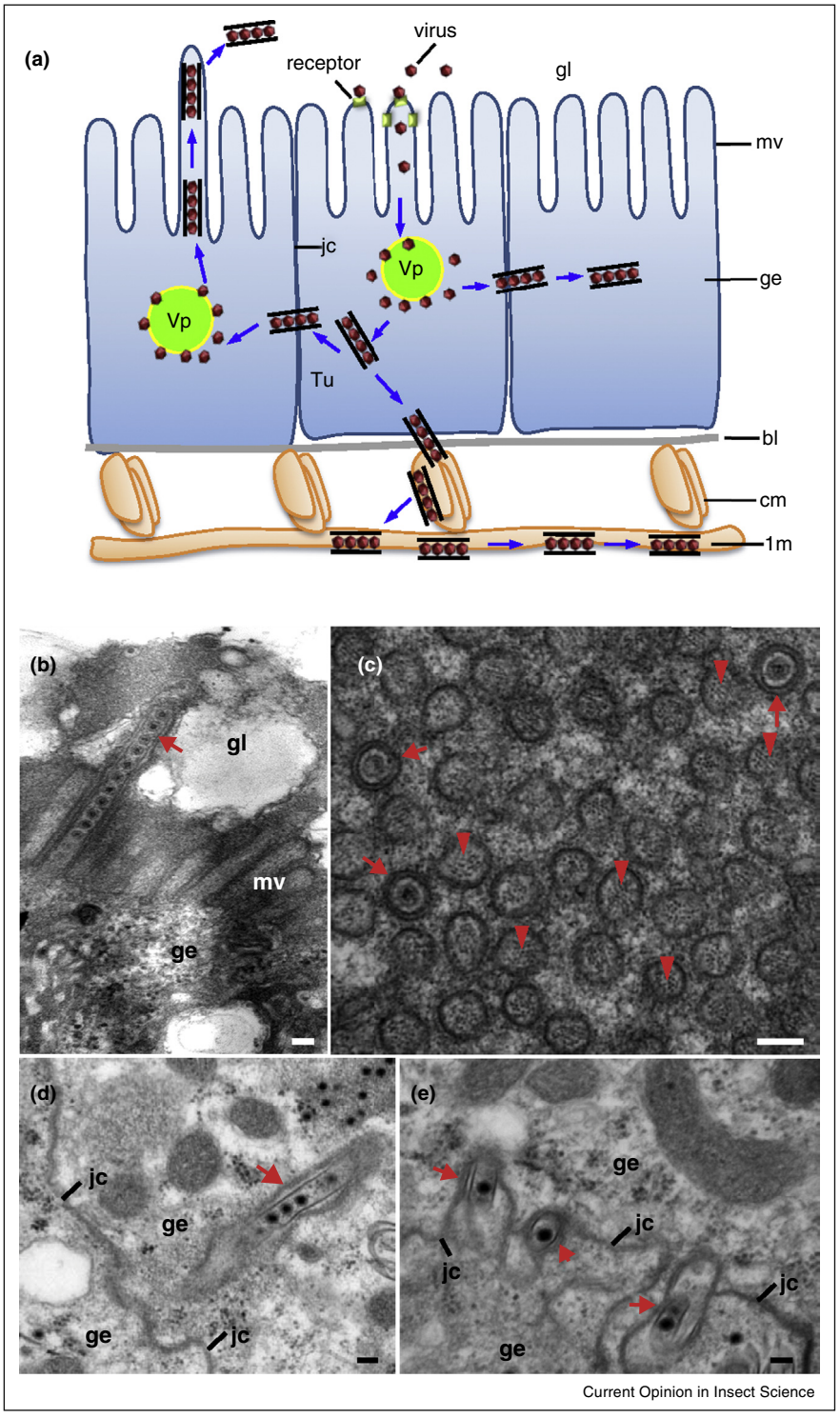
Propagative plant viruses of agricultural importance include plant reoviruses, plant rhabdoviruses, tospoviruses, tenuiviruses, and marafiviruses, mainly transmitted by sap-sucking insects, primarily leafhoppers, planthoppers, aphids and thrips [1,2,3]. These viruses infect and replicate in their insect vectors and are retained by the insects throughout their life, even after molting. While propagating in the insect vectors, viruses circulate through the insect bodies, from the gut *via* the hemolymph to other organs or the salivary glands, from where virions are ejected into the plant host during insect feeding [1,2,3]. The insect gut consists of a monolayer of epithelial cells, lined on the lumen side with protruding microvilli appearing as a brush border and covered on the outer side with the basal lamina, that are connected by intercellular junctional complexes (Figure 1) [4]. The gut barrier is the principal determinant for the ability of an insect species to transmit a virus. In general, the microvilli, intercellular junctions, and basal lamina of insect gut act as barriers for viral entry and dissemination.

Initial entry of viruses into the gut epithelium

Microvilli of the insect gut are cellular membrane protrusions of the epithelium [5]. The gut microvillar membrane contains cellular receptors for the initial attachment and entry of viruses. Propagative plant viruses, once ingested by the insects, accumulate in the gut lumen, and then infect the epithelial cells through the microvillar membranes [6,7••,8,9,10]. However, only a limited number of epithelial cells contain receptors on the microvillar membranes for propagative plant viruses to attach [6,7••,8,9,10]. By contrast, almost all gut microvilli contain cellular receptors for persistent nonpropagative plant viruses such as begomoviruses and luteoviruses to attach [2,11]. In fact, the multiplication of propagative plant viruses for producing more progeny virions in initially infected epithelial cells is essential for compensating for the insufficiency of invading viruses from the gut lumen.

Insect vector cell lines can allow us to trace the early entry process of propagative plant viruses at the cellular level. During the past 30 years, primary or continuous cell cultures derived from leafhoppers, planthoppers and aphids and thrips, originally initiated from embryonic fragments of insect eggs, have been established to support the persistent replication of propagative plant viruses [12,13,14,15,16,17]. Rice dwarf virus (RDV), a plant reovirus, is the best-characterized plant virus regarding entry into its leafhopper vector cells, because the structures of the mature virion and minor outer capsid protein P2 have been elucidated [18••,19]. RDV enters leafhopper cells through receptor-mediated, clathrin-dependent endocytosis and is sequestered in early endosomes [20]. RDV P2, which protrudes from the surface of the outer shell of virions, is involved in initial recognition and interaction with cellular receptors [18••,21]. RDV P2 has an L-shaped flexible structure with a 10-nm-long domain that is responsible for anchoring on the surface of virion and a 15-nm-long domain for contacting with an unknown cellular receptor(s) [18••]. The L-shaped structure of P2 has characteristics identical to the spike proteins of other plant reovirueses such as rice black streaked dwarf virus (RBSDV), south rice black streaked dwarf virus (SRBSDV), and rice ragged stunt virus (RRSV) [1,2]. The spike protein of RRSV *in vitro* binds to a 32-kDa cytomembrane protein of its brown planthopper vector,

Figure 1



Plant reoviruses exploit actin-based tubule motility to overcome gut epithelium barriers in the vector insects. **(a)** Model for the motility of virus-containing tubules in insect gut epithelium. Initially, viral particles recognize and bind to cellular receptors on the microvillar membrane, and then enter the gut epithelium. The viruses then propagate in the viroplasm for assembly of progeny virions and synthesis of virus-containing tubules. These tubules can pass through microvilli of the epithelium into the lumen or across the basal lamina from the epithelium into the visceral circular muscle, then spread through the external longitudinal muscle, or cross the tight junctions between epithelial cells to facilitate viral cell-to-cell spread. Blue arrows indicate the process of viral infection. **(b)** Electron micrograph showing the elongated tubule-associated microvillus (arrow) has formed membrane protrusion toward the gut lumen in RDV-infected leafhopper. **(c)** Transverse section of microvilli of about 100 nm in