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Neurohormones implicated in the control of Malpighian tubule secretion in plant sucking heteropterans: The stink bugs *Acrosternum hilare* and *Nezara viridula*

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ABSTRACT

Plant sucking heteropteran bugs feed regularly on small amounts of K^+-rich plant material, in contrast to their hematophagous relatives which imbibe large volumes of Na^+-rich blood. It was anticipated that this would be reflected in the endocrine control of Malpighian tubule (MT) secretion. To explore this, neuroendocrine factors known to influence MT secretion were tested on MT of the pentatomid plant sucking stink bugs, *Acrosternum hilare* and *Nezara viridula*, and the results compared with previously published data from *Rhodnius prolixus*. Serotonin had no effect on *N. viridula* MT, although it stimulates secretion by *R. prolixus* MT >1000-fold, and initiates a rapid diuresis to remove excess salt and water from the blood meal. Kinins had no effect on stink bug MT, but secretion was increased by Zoone-DH, a CRF-like peptide, although the response was a modest 2–3-fold acceleration compared with 1000-fold in *R. prolixus*. Native CAPA peptides, which have diuretic activity in dipteran flies, had antidiuretic activity in MT of the stink bug (Acrhi/Nezvi-CAPA-1 and -2), as previously shown with Rhopr-CAPA-2 in *R. prolixus*. The antidiuretic activity of Rhopr-CAPA-2 has been linked with terminating the rapid diuresis, but results with stink bugs suggest it is a general feature of heteropteran MT.

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1. Introduction

Heteropteran insects (the "true" bugs) have sucking mouth parts and are obligate fluid feeders. The majority feed on plant material or other insects, but some, such as the kissing bug *Rhodnius prolixus* (Heteroptera; Triatomidae), feed on the blood of vertebrates. Plant sucking bugs feed regularly and take relatively small fluid meals, whereas their hematophagous relatives feed irregularly and may imbibe blood meals that are so large the insect is rendered virtually immobile. The different feeding habits of plant sucking and blood sucking bugs impose different requirements on the excretory system for the maintenance of body fluid homeostasis, and this is likely to be reflected in the hormonal control of Malpighian tubule (MT) secretion. This has been intensively studied in *R. prolixus*, but little is known about the control of MT secretion in plant sucking bugs.

R. prolixus consumes blood meals equivalent in volume to 10–12 times the unfed body weight. To regain maneuverability and to concentrate nutrients (blood cells) in the gut, much of the imbibed plasma (NaCl and water) is rapidly absorbed into the hemolymph from the expanded anterior midgut (a functional crop), transported into the lumen of the upper (secretory) segment of the MT, and voided as NaCl-rich urine from the anus. The rapid diuresis lasts about 3 h, during which time drops of urine are voided from the anus every 2–3 min, and about 50% of the imbibed salt and water are excreted. The volume and composition of the hemolymph change very little after feeding, because rates of absorption of NaCl-rich fluid from the blood meal in the anterior midgut and excretion of NaCl-rich urine are precisely matched.

Pioneering work by Simon Maddrell (reviewed in Ref. [2]) demonstrated that the rapid diuresis is initiated by release of a diuretic hormone (DH) released within seconds of the insect commencing to feed [16] from neurohemal sites on abdominal nerves originating from the fused mesothoracic ganglion mass (MTGM). The DH accelerates MT secretion >1000-fold and also stimulates fluid uptake from the anterior midgut [9], thereby ensuring that the two processes are closely coordinated.

In *R. prolixus*, the rapid diuresis is initiated by serotonin [13,18], which is released at neurohemal sites along axons that originate from five dorsal unpaired median (DUM) cells in the MTGM and project into the lateral abdominal nerves. The circulating titer of

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serotonin increases to >100 nM within 5 min of feeding [13], which is sufficient to maximally stimulate fluid uptake from the anterior midgut and MT secretion [2,9,17]. Serotonin levels fall after 5 min, and the rapid diuresis is sustained by release of a corticotropin releasing-factor (CRF)-like DH from the axons of posterior lateral neurosecretory cells in the MTGM that also project into the abdominal nerves [39]. A CRF-like DH of *R. prolixus* has yet to be identified, but Zoone-DH, a CRF-like peptide from the termite *Zootermopsis nevadensis*, maximally stimulates fluid transport across both the anterior midgut and the upper MT segment [38,40]. The rapid diuresis ceases after about 3 h, which was originally thought to be due to the removal of the stimulus for DH release and the degradation/excretion of circulating hormone. More recently, however, evidence has emerged for the release of an antidiuretic peptide toward the end of the rapid diuresis, which decreases stimulated rates of fluid transport across both the upper MT and the anterior midgut [29,36]. This peptide belongs to the family of cardioacceleratory 2b (CAP_{2b}) peptides, which are designated CAPA peptides, because they are encoded on the *capability* (*capa*) gene (capable of encoding CAP_{2b}) of the fruit fly, *Drosophila melanogaster*. The *capa* gene of *R. prolixus* is expressed in three bilaterally paired cells on the ventral surface of the MTGM, and CAPA-like immunoreactive material is released from their axons, which project into the abdominal nerves, toward the end of the rapid diuresis [31,32].

In contrast to *R. prolixus*, plant sucking bugs feed on material with low salt content and do not imbibe large volumes of fluid. The rapid diuresis and natriuresis that enables the speedy removal of much of the volume and salt load consumed by *R. prolixus* is therefore inappropriate for a plant sucking insect. The only study to date of MT function in a plant sucking heteropteran [20] focussed on the handling of the cardiac glycoside ouabain by the large milkweed bug *Oncopeltus fasciatus* (Heteroptera; Lygaeidae). Little is known of the control of MT secretion in plant sucking bugs, but serotonin appears to be a neurohormone in *O. fasciatus*, although the serotonergic DUM cells that are found in *R. prolixus* are absent [21]. Moreover, serotonin does not stimulate cAMP production by *O. fasciatus* MT, although this is the diuretic second messenger in *R. prolixus*. The plant sucking bug may, therefore, not use serotonin as a DH, which is consistent with it not requiring the rapid diuresis of its blood feeding relative.

The present study examines the control of MT secretion in two related plant sucking bugs (Heteroptera: Pentatomidae), the green stink bug *Acrosternum hilare*, and the Southern green stink bug *Nezara viridula*, polyphagous pentatomids that have a detrimental effect on product quality and yield in cotton and other row, fruit and nut crops [33]. More recently, adult southern green stink bugs have been shown to vector plant pathogens in cotton [19]. These bugs feed by inserting their proboscis into the host plant and sucking up nutrients. They employ a macerate-and-flush strategy [10]; the mandibular and maxillary stylets contained within the proboscis sheath cut into the plant and saliva, which contains digestive enzymes, is injected into the wound to liquefy the tissues [19]. The macerated and partially digested material is "flushed out" by the saliva and ingested by sucking. Relatively small volumes of liquefied material, much of which is the injected saliva, are imbibed and there is little obvious abdominal distension during feeding. In this paper, attention has focussed on the effects of serotonin and of neuropeptides implicated in the control of MT secretion, namely kinin, CRF-related peptides and CAPA peptides. Kinin and CRF-related peptides have yet to be identified from stink bugs, but two CAPA peptides (Nezvi-CAPA-1 and -2) are known from *N. viridula* [34] and identical peptides are present in *A. hilare* [35]. The effect of CAPA peptides on stink bug MT was of particular interest since these peptides have diuretic activity in dipteran insects [6,22,27,26], but antidiuretic activity in *R. prolixus*. The immunocytochemical localization of CAPA cells in *N. viridula* is identical to that described in *R. prolixus* and the presence of neurohemal release sites on the abdominal nerves suggests CAPA peptides function as circulating hormones.

2. Materials and methods

2.1. Insects

Adult green stink bugs (*A. hilare*) were captured in 40 W light traps (with live insect canisters) located adjacent to fields cultivated with corn, cotton, sorghum and soybeans in Burleson County, Texas. Adult Southern green stink bugs (*N. viridula*) were obtained from a colony maintained at the USDA Invasive Insects Biocontrol & Behavior Laboratory, Beltsville Agricultural Research Center in Beltsville, MD.

2.2. Fluid secretion assay

Stink bugs have four MTs that are situated in the dorsal abdomen with their closed distal ends surrounding the heart. Female bugs were fixed ventral side uppermost in a wax dish. The dish was then flooded with *O. fasciatus* saline [20] (Table 1) and the ventral abdominal sterna cut away. The ovaries were removed and the gut carefully pulled to one side to expose the two ureters each with an attached pair of MT. Although it was possible to dissect out intact MT this was an extremely slow process and, in general, studies were made using shorter lengths (~1.5 cm) that did not include the most distal (from the gut) closed ends of the tubules. A length of MT was removed by gripping the region closest to the ureter with a pair of watchmaker's forceps, cutting it away from the ureter, and then gently teasing it free of tracheal connections using a fine glass rod. Once a sufficient length of tubule was dissected free it was severed and transferred to a 10 μl drop of *O. fasciatus* saline resting on the Sylgard-lined based on a Petri dish containing water-saturated paraffin oil. Each end of the tubule segment was withdrawn into the surrounding paraffin oil and wrapped around separate minutin pins set close to the drop of bathing fluid. With practice, all four MTs could be removed from an insect in <10 min.

Stink bug MT secreted spontaneously in *O. fasciatus* saline, and fluid generally emerged only from the lower end of the tubule which would have emptied into the ureter. Secreted droplets were collected using a fine glass micropipette at 20–40 min intervals when the bathing fluid was replenished. The collected fluid was discharged under the paraffin oil and droplet diameter (D) measured with an eyepiece micrometer. The volume (V) of the secreted droplets could then be calculated ($V = D^3\pi/6$) assuming they were perfect spheres when resting on the non-wettable Sylgard. Rates of secretion (in nL min^{-1}) were obtained after dividing the volume (in nL) by the time interval over which the droplet was collected. For *A. hilare* MT, basal rates of secretion were measured over 60 min before they were challenged with test substances dissolved in *O. fasciatus* saline. To correct for differences in the rate of secretion by MT of different lengths, the effects of test

Table 1
Composition of *O. fasciatus* saline [17].

	Concentration (mM)
NaCl	20
KCl	24
$MgCl_2$	2
$CaCl_2$	2
NaH_2PO_4	2.5
Na_2HPO_4	3.5
Glucose	6.7

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