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Chemosensory Basis of Host Recognition in Butterflies—Multi-component System of Oviposition Stimulants and Deterrents

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Introduction

Larvae of most butterfly species feed on a limited number of host species belonging to a single plant family. The choice of host plants is determined both at the egg-laying and larval-feeding stages (Schoonhoven *et al.*, 1998). The choice of oviposition site by an adult female is crucial to the survival of their offspring, and thus the mother butterflies lay their eggs with great precision on the host plants. Although host recognition by phytophagous insects involves multiple sensory modalities, including visual, olfactory and gustatory cues, contact chemical stimuli from host and non-host plants play an important role at the final step of egg-laying behavior. The contact chemoreceptors responsible for detection of both host and non-host allelochemicals at oviposition are located on the foretarsi of the female butterfly (Roessingh *et al.*, 1991; Nishida, 1995).

Oviposition stimulants

In recent years, suites of specific host-finding cues have been characterized for several families of butterfly species including Papilionidae, Pieridae and Nymphalidae (Honda and Nishida, 1999). Oviposition stimulants of the citrus swallowtail butterfly, *Papilio xuthus* (Papilionidae) were found to consist of multiple components which included flavonoids (**1** and **2**), a nucleoside (adenosine), alkaloids (**3** and **4**), a cyclitol (**5**) and an amino acid derivative (**6**) (Nishida *et al.*, 1987; Nishida, 1995) (Figure 1). None of the individual components elicited oviposition responses alone. The specific activity was provoked only when these components were applied as a mixture. Synergistic effects among stimulant components can be seen in several papilionid species (Honda and Nishida, 1999). The butterflies seem to perceive a subset of ingredients simultaneously as

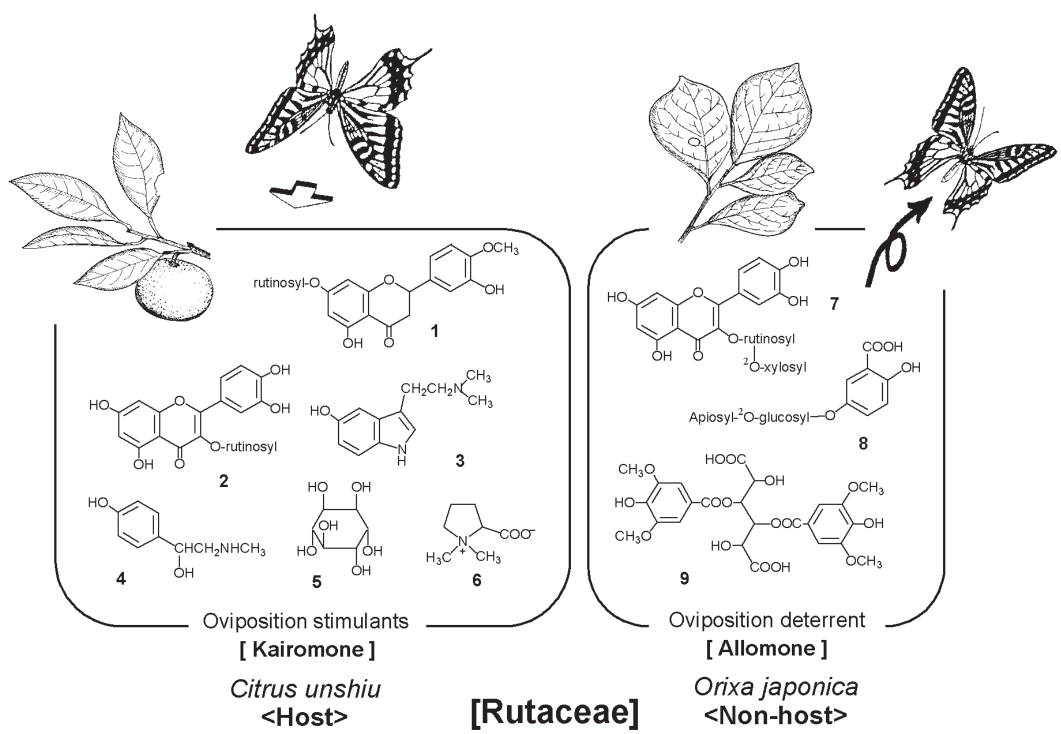

Figure 1 Multi-component systems of oviposition stimulants contained in a host plant, *Citrus unshiu* (left), and oviposition deterrents in a non-host rutaceous plant, *Orixa japonica* (right), for a Rutaceae-feeding swallowtail butterfly, *Papilio xuthus*. **1**, hesperidin; **2**, rutin; **3**, bufotenine; **4**, synephrine; **5**, *chiro*-inositol; **6**, stachydrine; **7**, quercetin 3-*O*-(2^G-β-D-xylopyranosylrutinoside); **8**, 5-{[2-*O*-(β-D-apiofuranosyl)-β-D-glucopyranosyl]oxy}-2-hydroxybenzoic acid; and **9**, disyringoyl aldaric acid ester.

a 'blend taste' with the toothbrush-like chemosensilla densely distributed on the tarsal segments. However, its sensory mechanism—how the butterfly integrates the complex signal arising from the many components—remains unknown. We do not know whether the stimulants are perceived simultaneously as a chemical blend on each sensillum or separately with each specific chemoreceptor cell. A multi-component system of oviposition stimulants seems to provide a high specificity in host recognition. On the other hand, it also provides some flexibility in host choices, allowing them to lay eggs not only on *Citrus* but also on rutaceous hosts belonging to other genera (e.g. *Poncirus* and *Xanthoxylum*) that partially share some common subsets of ingredients (unpublished data). Related swallowtail species such as *P. protenor* and *P. polyxenes* (Feeny *et al.*, 1988; Honda, 1990) also use the same classes of chemicals as the host-finding cues (e.g. flavonoid glycosides, phenethylamines and quinic acid derivatives). Such underlying chemical similarity may have provided a route to colonization on novel hosts among the papilionid butterflies (Feeny *et al.*, 1988; Nishida, 1995; Honda and Nishida, 1999).

Oviposition deterrents

Although *P. xuthus* feed on various rutaceous species, both the adult females and the larvae reject a rutaceous plant, *Orixa japonica*. A flavonoid triglycoside (**7**) was identified as one of the oviposition deterrents (Figure 1). Compound **7** is a xylosyl derivative of rutin (**2**), a positive stimulant for the butterfly (Nishida *et al.*, 1990). This compound may disrupt the oviposition stimulant activity due to its structural resemblance and relatively high concentrations in the leaves, competing for the same receptor cells. Two hydroxybenzoic acid derivatives (**8** and **9**) were characterized as potent deterrents at both oviposition and larval feeding (Ono *et al.*, 2004). Simultaneous occurrence of these compounds in *O. japonica* appears to provide an effective chemical barrier against the butterfly. Kairomones (stimulants) and allomones (deterrents) responsible for host recognition stimulate specific receptor cells in the tarsal chemosensilla of butterflies (Roessingh *et al.*, 1991). It remains unclear, however, whether these deterrent compounds block the intrinsic activity of the stimulants or exert their effect by other mechanisms in *P. xuthus*.

Larval gustatory responses to plant allelochemicals

The chemosensory mechanisms of oviposition and larval feeding must be intrinsically coordinated, for females usually select the plants the larvae accept. However, the nature of such gustatory responsiveness to allellochemicals at both larval and adult stages is not well understood. The fact that both oviposition and larval feeding are elicited (or deterred) by the same subset of chemicals suggests a congruent sensory mechanism between the tarsal chemoreceptors of adults and the gustatory chemoreceptors of larvae (Nishida, 1995; Ono *et al.*, 2004). Electrophysiological responses of the host kairomones and non-host allomones were examined against tarsal and larval mouthpart chemosensilla in *P. xuthus*. Both larval feeding stimulant (e.g. quinic acid) and deterrent (e.g. gentisic acid glycoside **8**) components evoked large numbers of spikes, probably stimulating different receptor cells of medial and lateral styloconic sensilla of the fifth instar larvae (unpublished). A comparison of the chemosensory components used by these butterflies to make food and oviposition choices reveals their evolutionary route to chemosensory adaptation at the insect–plant interface.

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