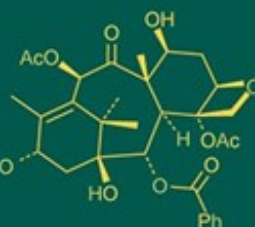
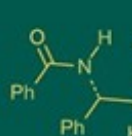
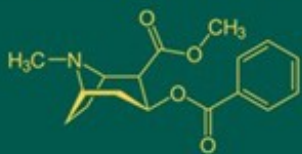


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Mulberry & silkworm: The chemistry behind a remarkable plant–insect relationship

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ABSTRACT

The mulberry silkworm, *Bombyx mori*, exhibits a highly specialized feeding relationship with mulberry (*Morus* spp.), which is regulated by a combination of volatile and non-volatile chemical cues, sensory receptors, feeding stimulants and physiological adaptations. Silkworm feeding behaviour can broadly be considered as a sequential process involving attraction, biting and swallowing. During the attraction phase, volatile compounds released from mulberry leaves stimulate the olfactory system and guide larvae towards the host plant. Among the identified volatiles, *cis*-jasmone has been demonstrated as a potent attractant, with BmOr-56/BmOR₅₆ functioning as an important olfactory receptor involved in its detection. Following contact with the leaf, non-volatile compounds including chlorogenic acid, isoquercitrin, morin, quercetin glycosides and β -sitosterol contribute to host recognition and test biting. Sugars such as sucrose and myo-inositol subsequently promote persistent biting and continued food intake. Genetic studies have further demonstrated that gustatory receptors such as GR₆₆ contribute substantially to the characteristic mulberry preference of *B. mori*. In parallel, the silkworm has evolved physiological mechanisms that enable it to tolerate defensive compounds such as 1-deoxynojirimycin (DNJ) present in mulberry. Thus, silkworm feeding represents a sophisticated interaction involving plant volatiles, gustatory chemicals, sensory receptors, genes, digestive physiology and microbial associations.

Keywords: *Bombyx mori*, Mulberry, Host-plant recognition, *Cis*-jasmone, BmOR₅₆, GR₆₆, β -sitosterol, Chlorogenic acid, DNJ, Feeding behaviour

Introduction

The mulberry silkworm, *Bombyx mori*, has a remarkable relationship with its food plant, mulberry (*Morus* spp.). Unlike Eri, Muga and Tasar silkworms that can feed on a wide range of host plants, the mulberry silkworm shows a strong preference for mulberry leaves. This specialized feeding behaviour is one of the most fascinating examples of plant–insect interaction (Kang *et al.*, 2019; Lu *et al.*, 2021) [1, 2]. Two step verification process is there before host plant selection, In the first screening step of detection of edible leaves, *B. mori* larvae demonstrate chemotaxis behaviour by using olfaction (Iizuka *et al.*, 2024) [3]. Once they reach their target leaves, a biting action is initiated, and swallowing factor such as cellulose, phosphate, and silica in leaves aids the larvae in the continuous consumption of food.

Mulberry: More than just a food plant

For a silkworm, a mulberry leaf is much more than a source of nutrients. It is a complex chemical package containing carbohydrates, proteins, amino acids, minerals, vitamins, sterols and secondary metabolites, which collectively influence feeding, growth and development. Some of these compounds act as feeding stimulants, while others may serve as chemical cues for host recognition. The silkworm therefore evaluates the leaf through a sophisticated chemosensory system rather than simply responding to its appearance. In *B. mori*, compounds such as chlorogenic acid, isoquercetin and β -sitosterol present in mulberry are involved in the recognition and stimulation of feeding (Lu *et al.*, 2021; Sato, 2024) [2, 4].

The larva possesses specialized chemosensory structures, particularly the maxillary palps and other mouthpart and body sensilla, containing gustatory receptors that help distinguish suitable food from unsuitable plants. Recent studies describe this as a two-step authentication process: first, the maxillary palps contact the leaf surface and detect trace amounts of mulberry-specific compounds such as chlorogenic acid, isoquercetin and β -sitosterol; this is followed by a test bite, during which sugars and other compounds released from the leaf tissue provide additional information about its suitability. Receptors such as BmGr₆, BmGr₉ and BmGr₆₃ have been shown to participate in the recognition of feeding-promoting compounds, demonstrating how chemical signals from mulberry are translated into the behavioural response of biting and sustained feeding (Kang *et al.*, 2019; Yang *et al.*, 2022; Sato, 2024) [1, 4].

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The invisible signals released by mulberry

Plants continuously release a variety of volatile organic compounds (VOCs) into their surroundings. These airborne chemical signals play an important role in plant–insect communication and can influence insect behaviour. For *Bombyx mori*, such signals provide information about the presence and possible location of a suitable food plant. The larva detects these volatile cues through its olfactory system and moves towards the source, a directed response commonly described as chemotaxis. This initial olfactory recognition represents the first stage in the silkworm's interaction with its host plant and helps it distinguish potential food sources before physical contact with the leaf (Tanaka *et al.*, 2009; Lu *et al.*, 2021) [5, 2].

Once the larva reaches the mulberry leaf, the feeding decision involves a second level of chemical evaluation. Non-volatile compounds present on the leaf surface and within the leaf tissue are detected through specialized gustatory structures associated with the mouthparts. These chemical cues help the larva determine whether the leaf is suitable for feeding and can stimulate biting and continued ingestion. In addition to chemical cues, the physical characteristics of the leaf and its nutritional composition influence feeding and subsequent utilization of the food. Thus, the interaction between *B. mori* and mulberry involves a coordinated sequence of olfactory attraction, gustatory recognition, biting, ingestion and nutritional utilization, demonstrating the remarkable precision with which the silkworm identifies and consumes its preferred food plant (Kang *et al.*, 2019; Lu *et al.*, 2021) [1, 2].

Three phases of silkworm feeding

1. Attracting factors – the pre-bite phase

Several volatile compounds have been reported to contribute to the attraction of silkworm larvae, including:

- Cis-Jasmone
- Citral
- Linalool and Linalyl acetate
- Terpinyl acetate
- Hexenol / Hexenal, commonly referred to as leaf alcohol/aldehyde

These compounds are therefore considered part of the volatile odour profile of mulberry, which provides information to the larva before it physically contacts the leaf. (Hamamura *et al.*, 1961; Lu *et al.*, 2021) [6, 2].

From a scientific perspective, these compounds should not be considered as independent or exclusive determinants of mulberry attraction. Under natural conditions, the silkworm encounters a mixture of volatile compounds, and its response depends on the composition and concentration of this chemical blend. Subsequent studies have demonstrated that *B. mori* possesses highly specialized olfactory receptors capable of detecting particular mulberry volatiles, providing a molecular basis for chemotactic behaviour (Tanaka *et al.*, 2009; Tanaka *et al.*, 2023) [5]. Thus, the combined action of mulberry volatiles can be viewed as an initial chemical “address” that helps the silkworm locate its preferred host plant. Once the larva reaches the leaf, the feeding decision shifts from airborne olfactory cues to contact-based gustatory and nutritional cues that regulate biting and continued consumption (Lu *et al.*, 2021) [2].

2. Biting factors – the feeding initiation phase

- β -Sitosterol: A major plant sterol that contributes significantly to the stimulation of biting and feeding behaviour in silkworm larvae.
- Flavonoids: Isoquercitrin and Morin
- Chlorogenic Acid (CGA)

Once the silkworm larva reaches the mulberry leaf, non-volatile chemical constituents present on the leaf surface and within the leaf tissue provide the next level of information for host recognition. Early

feeding studies identified β -sitosterol and flavonoids such as isoquercitrin as important biting stimulants, while morin was also reported to possess biting-stimulating activity (Nayar *et al.*, 1962; Hamamura *et al.*, 1962) [8, 7]. β -Sitosterol isolated from mulberry was subsequently shown experimentally to stimulate feeding in *B. mori*, although the study also demonstrated that sterols have both nutritional and phagostimulatory roles (Ito *et al.*, 1964) [9]. These findings established that the larva does not begin sustained feeding simply because it has reached a green leaf; rather, specific chemical constituents are detected by its sensory system and contribute to the initiation of biting.

More recent research has provided a molecular explanation for these observations. Ueno *et al.* (2020) demonstrated that the maxillary palps of *B. mori* function as highly sensitive chemosensory organs during the first stage of host acceptance. Neurons in these palps can detect extremely small quantities of chlorogenic acid, quercetin glycosides and β -sitosterol on the leaf surface; detection of this combination promotes a test bite. After the test bite, chemicals released from the leaf tissue, particularly sugars, are evaluated by sensory neurons associated with the mouthparts, allowing the larva to decide whether to proceed to persistent feeding. Thus, the earlier concept of “biting stimulants” has now been refined into a two-stage host-acceptance mechanism, in which surface chemical cues trigger test biting and tissue-derived nutritional cues help sustain continuous feeding (Ueno *et al.*, 2020; Sato, 2024) [4, 10].

3. Swallowing factors – the continuous consumption phase

Important factors associated with this phase include:

- Cellulose
- Silica
- Potassium Phosphate
- Sugar alcohols - Myoinositol and Sucrose

Initiation of biting does not necessarily ensure continuous food intake. Once the leaf tissue is masticated and enters the mouth, gustatory signals generated from soluble nutrients help activate and regulate the swallowing response. Among the compounds investigated, sucrose has particularly strong experimental support. Sasaki *et al.* (2006) [11] demonstrated that sucrose applied to the mouthparts of *Bombyx mori* larvae directly triggered swallowing movements, and higher sucrose concentrations increased the rate of ingestion and strengthened the rhythmic contractions of the cibarial pump. Earlier feeding experiments also showed that sucrose was one of the strongest feeding stimulants among the sugars and related compounds tested (Ito, 1960). These findings indicate that soluble nutrients do not merely provide nutritional value after ingestion; they can also act as sensory signals that promote the transition from biting to ingestion.

Myo-inositol provides another important example of a nutrient-associated feeding signal. Electrophysiological studies identified specific sensory neurons and the gustatory receptor *BmGr₁₀* that respond to myo-inositol, demonstrating that the silkworm possesses a dedicated sensory mechanism for detecting this compound (Koh *et al.*, 2016) [12]. Furthermore, Sasaki *et al.* (2013) [13] showed that a combination of myo-inositol and sucrose enhanced feeding activity and modified both chewing and swallowing motor patterns, suggesting that these compounds can influence the neural circuits controlling ingestion. A recent review also confirms that myo-inositol functions as a feeding-inducing factor in silkworm larvae (Sato, 2024) [4]. The roles of cellulose, silica and phosphate/mineral components should be described more cautiously. Earlier nutritional studies reported that cellulose could enhance feeding when incorporated into artificial diets, suggesting that physical or nutritional properties of the diet can influence feeding behaviour (Ito, 1960). However, current molecular studies of *B. mori* feeding focus much more strongly on soluble sugars, myo-inositol and other gustatory stimuli and on the neural mechanisms controlling chewing and swallowing. Therefore, rather than stating that cellulose, silica and potassium phosphate are established swallowing stimulants, it is scientifically safer to describe them as dietary or

physical factors that may contribute to the suitability and continued ingestion of plant material, while giving stronger emphasis to sucrose and myo-inositol as experimentally demonstrated feeding/swallowing-related signals

Potent attractant

The chemical invitation: *cis*-jasmone

Volatiles emitted by green leaves trigger chemotaxis behaviour in the insects, in silkworm *Bombyx mori* chemotaxis behaviour is majorly driven by potent attractant named as *cis*-jasmone. *Cis*-jasmone is a derivative of the plant hormone jasmonic acid and is synthesized as a metabolite from linolenic acid via the octadecanoid pathway. Researchers analysed volatile compounds emitted from mulberry leaves and tested their ability to attract silkworm larvae. Among the compounds examined, *cis*-jasmone showed particularly strong attraction. Remarkably, behavioural experiments demonstrated a response to extremely small quantities: the threshold amount required to elicit attraction from a distance of 20 cm was approximately 0.3 pg for *cis*-jasmone, 3 pg for *trans*-jasmone, 30 pg for dihydrojasmone and 300 pg for 2-amylcyclopentenone. Thus, *cis*-jasmone showed the highest potency among the compounds tested, with attraction occurring at an extremely small quantity. These results demonstrate the exceptional sensitivity of the silkworm olfactory system and highlight the importance of volatile chemical cues in host-plant localization before physical contact with the leaf (Tanaka *et al.*, 2009) [5].

The receptor: *BmOr-56*

The silkworm possesses a specialized odorant receptor called *BmOr-56*, which is remarkably sensitive to *cis*-jasmone, allowing the insect to detect even tiny amounts of this volatile chemical released by mulberry leaves. Studies examining olfactory receptor genes expressed in larval olfactory organs identified *BmOr-56* as highly responsive to *cis*-jasmone (Tanaka *et al.*, 2009; Morinaga *et al.*, 2023) [5, 14]. Functional experiments showed that the receptor has a strong sensitivity to this compound, and the receptor response corresponded closely with the behavioural attraction observed in silkworm larvae. Thus, *BmOr-56* can be viewed as an important molecular component of the silkworm's *cis*-jasmone detection system. Scientists generated silkworms in which *BmOr-56* was deleted using gene-editing technology. These mutant silkworms lost the attractive behavioural response to *cis*-jasmone, providing direct genetic evidence that *BmOr-56* plays a critical role in this specific chemoattraction. Among a total of 66 Ors identified in the *B. mori* genome, we found that 23 were expressed in the olfactory organs during larval stages.

Potent gustatory stimulant

Finding a plant is only the first step. The silkworm must also decide whether the leaf is suitable for feeding. This is where gustatory receptors become important. Chemical compounds present in mulberry leaves interact with sensory receptors associated with feeding behaviour. Some compounds act as phagostimulants, encouraging the larva to bite and continue feeding. Major plant sterols present in mulberry is β -sitosterol which act as a Gustatory stimulant. The feeding response is determined by a combination of compounds rather than by one chemical alone (Nayar & Fraenkel, 1962; Ueno *et al.*, 2020; Sato, 2024) [8, 4, 10]. Instead, it is the result of a complex chemical profile containing several compounds that together make mulberry highly acceptable to *B. mori*. Mulberry leaves provide proteins and amino acids needed for tissue development and enzyme synthesis, carbohydrates that provide energy, lipids and sterols required for physiological processes, and minerals and other micronutrients required for normal development.

The genetic switch: *GR66*

Perhaps the most striking evidence for the genetic control of mulberry preference came from studies of the gustatory receptor gene *GR66*. In 2019, Zhang *et al.*, used CRISPR/Cas9-mediated gene editing to dis-

rupt *GR66* in *Bombyx mori*. *GR66* encodes a putative bitter gustatory receptor. The result was remarkable. Silkworms strongly preferred mulberry and generally rejected several other plant materials. However, silkworms carrying mutations in *GR66* lost much of their normal mulberry specificity and began feeding on a surprisingly broad range of materials, including apple, pear, soybean, corn and other plants. This provided powerful experimental evidence that a specific gustatory receptor can have a major influence on host-plant preference.

The chemosensory neurons in the maxillary palp (MP) of the larvae detect mulberry secondary metabolites, chlorogenic acid (CGA), and isoquercetin (ISQ), with ultrahigh sensitivity, for host plant recognition and feeding initiation. *BmGr6* is regarded as a putative sugar receptor and *BmGr9* was reported as a fructose receptor, we investigated their response to major sugars present in the mulberry leaves (D-fructose, D-glucose, sucrose, and myo-inositol). results indicate that the two Grs are highly tuned to CGA and ISQ, whereas *BmGr9* also exhibits a high affinity with D-fructose.

The fascinating defence system of mulberry

Mulberry provides food to the silkworm, but at the same time, the plant has evolved its own defence mechanisms against herbivores. Plants cannot run away from insects that feed on them. Instead, they defend themselves through physical barriers and chemical compounds known as secondary metabolites. Mulberry is particularly interesting because it contains 1-deoxynojirimycin (DNJ), a naturally occurring iminosugar (azasugar) characteristic of *Morus* species. DNJ closely resembles the structure of glucose and can therefore interact with carbohydrate-digesting enzymes. Studies have demonstrated that DNJ is a potent inhibitor of α -glucosidases, enzymes involved in the breakdown of dietary carbohydrates into absorbable sugars. This biochemical property can interfere with carbohydrate digestion and has made DNJ one of the best-studied bioactive compounds in mulberry (Wang *et al.*, 2021; Liu *et al.*, 2015) [16, 15].

Interestingly, DNJ may also have an ecological role beyond its biochemical activity. Comparative studies of *Morus alba* have reported that DNJ possesses antifeedant activity against some insects, suggesting that it may contribute to the plant's chemical defence. However, this effect is not universal, and *B. mori* is highly specialized for feeding on mulberry. Thus, rather than describing DNJ simply as a "defence compound," it is more accurate to view it as one component of the complex chemical environment of mulberry that can influence herbivore physiology and feeding interactions (Yagi *et al.*, 1976, Liu *et al.*, 2015) [17].

Conclusion: A remarkable chemical partnership

The relationship between *Bombyx mori* and mulberry is a beautiful example of nature's chemical engineering. Mulberry provides nutrients and chemical cues that help the silkworm recognize and utilize its host plant. At the same time, the plant produces defensive compounds such as DNJ, while the silkworm has evolved physiological mechanisms that allow it to thrive on its specialized food plant. Volatile compounds such as *cis*-jasmone demonstrate how plants can communicate chemically with insects, while compounds such as β -sitosterol, Morin and other leaf constituents contribute to the complex nutritional and physiological environment experienced by the insect. Ultimately, the silkworm's preference for mulberry is the outcome of sensory recognition, feeding stimulation, nutritional suitability and long-term evolutionary adaptation.

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