## Review Article

## Decoding Silkworm–Host Plant Interactions: A Comprehensive Review of Chemosensory and Genetic Mechanisms in Bombyx mori and Antheraea assamensis

**ABSTRACT**

Understanding the intricacies of silkworm–host plant interactions is pivotal for advancing sustainable sericulture and improving silk productivity. This review comprehensively examines the behavioral, chemical, and molecular mechanisms governing host plant recognition and feeding in *Bombyx mori* (monophagous) and *Antheraea assamensis* (polyphagous). We detail how silkworm larvae rely on a sophisticated two-step chemosensory process involving maxillary palp and galea, with specialized gustatory receptors responding to stimulants such as chlorogenic acid, β-sitosterol, and sucrose. In *B. mori*, feeding is highly selective, driven by gustatory and olfactory receptor genes like *Gr66*, *Gr6*, and *Gr9*, which enforce mulberry specificity. Gene-editing studies reveal that these receptors act as molecular gatekeepers of host fidelity. Conversely, *A. assamensis* exhibits broader chemosensory plasticity, accepting a range of Lauraceae species due to a more diverse receptor repertoire and less stringent phytochemical thresholds. We also explore the role of phytochemicals in muga host plants such as *Persea bombycina*, and highlight the need for functional genomics studies to decode the sensory basis of polyphagy in non-mulberry silkworms. Insights from this review offer new avenues for artificial diet development, genetic improvement of silkworm strains, and sericultural resource optimization. Furthermore, comparative findings between monophagy and polyphagy contribute to our broader understanding of insect–plant co-evolution and sensory ecology.

*Keywords: Silkworm–host plant interaction, Bombyx mori, Antheraea assamensis, chemosensory receptors, host specificity, monophagy, polyphagy, gustatory genes, molecular feeding mechanisms*

## ****INTRODUCTION****

Sericulture is a traditional agro-based industry that integrates the cultivation of host plants, rearing of silkworms, and the processing of cocoons through reeling and spinning to produce high-quality silk yarn. It is widely recognized for its sustainability, labor-intensive nature, and socio-economic importance, particularly in developing nations such as India and China. With its potential to generate quick financial returns within a short span, sericulture has become an increasingly vital source of income for rural and semi-urban populations. The industry is broadly classified into two main sectors based on the feeding behavior and host plant specificity of silkworms: mulberry and non-mulberry sericulture (Padaki *et al.,* 2014; Das *et al.,* 2020). The mulberry sector primarily involves the rearing of the domesticated silkworm Bombyx mori L. for producing fine, commercial-grade silk. In contrast, the non-mulberry sector includes the rearing of wild silkworms, or "vanya" silks, such as muga (Antheraea assamensis), eri (Samia ricini), tropical tasar (Antheraea mylitta), and temperate tasar (Antheraea proylei) (Saikia & Saikia, 2022).

The diversity of sericulture systems is closely tied to the feeding behavior of silkworms, which, in turn, reflects a broader pattern observed across insect taxa. Insects constitute the most diverse and numerous animal groups on Earth, representing nearly 50–70% of all described species (Caers *et al.,* 2012; Belles, 2010). This biodiversity is largely shaped by their wide-ranging feeding ecologies and adaptive strategies across habitats (Song *et al.,* 2021). Insects can be broadly grouped based on dietary habits into phytophagous (plant-feeding), carnivorous, and omnivorous types (Regier et al., 2015). Within phytophagous insects, feeding specialization varies from strict monophagy, where insects feed on a single plant species to oligophagy and euryphagy, where insects consume a limited or wide range of plant taxa, respectively (Morris, 2007).

This variation in host plant use has profound implications for sericulture. The host plant not only serves as the primary food source but also directly influences silkworm physiology, growth, cocoon formation, and silk quality (Saranya *et al.,* 2019). Bombyx mori, being monophagous, feeds exclusively on mulberry (Morus spp.) leaves, which are nutritionally rich and capable of meeting the complete dietary needs of the silkworm (Fraenkel, 1959; Nagaraju, 2002; Fambayun *et al.,* 2022). The quality and availability of these leaves are therefore pivotal to successful silkworm rearing. Factors such as plant cultivar, leaf maturity, environmental conditions, and the concentration of secondary metabolites collectively determine the nutritional profile of the foliage. These variables significantly influence key biological traits in silkworms including larval survival, growth rate, cocoon yield, and filament quality (Samami *et al.,* 2019).

Silkworms, like other phytophagous insects, employ complex chemosensory systems to recognize, assess, and accept suitable host plants. The feeding process is initiated and regulated by a combination of physical characteristics (such as texture, shape, and color) and chemical cues, particularly plant volatiles and surface compounds (Miller & Strickler, 1984; Rausher, 1978; Renwick, 1990; Carter & Feeny, 1999). Host plant location is typically guided by olfactory and visual cues at long range, whereas tactile and gustatory perception becomes dominant at close range (Bernays & Chapman, 1994). Once the silkworm larva comes into contact with a leaf surface, its gustatory receptor neurons are activated to evaluate the presence of stimulatory or inhibitory compounds, thereby influencing feeding decisions (Watanabe, 1958; Thorsteinson, 1960; Ishikawa *et al,* 1969).

A substantial body of research has demonstrated the importance of secondary plant metabolites in mediating host plant selection and feeding behavior in lepidopteran larvae (Haynes *et al.,* 1991; Lopez *et al.,* 2000; Legay, 1958). Compounds such as phenolics, flavonoids, sterols, and terpenoids act either as phagostimulants, encouraging feeding, or as deterrents, depending on their concentration and the insect’s gustatory receptor response. In B. mori, specific chemicals like chlorogenic acid, isoquercetin, and β-sitosterol have been shown to elicit strong feeding responses and promote larval development (Ito & Tanaka, 1959; Nayar & Fraenkel, 1962; Neog *et al.,* 2011), highlighting the critical role of host plant chemistry in silkworm biology.

Further complicating this interaction is the role of adult female behavior in oviposition site selection. In insects with limited larval mobility, such as silkworms, the choice of oviposition site by the female strongly determines larval success. Females rely on a suite of environmental and chemical cues to locate optimal host plants that ensure suitable larval habitats and food resources (Gothard *et al.,* 2005; Bossart & Scriber, 1999). Therefore, the relative acceptability of a host plant is governed by a dynamic interplay of intrinsic factors such as genetic and neurophysiological makeup and extrinsic factors, including surface chemistry and plant volatiles (Sokame *et al.*, 2020; Scheirs *et al.,* 2000).

Among the diverse types of silk produced worldwide, mulberry and muga silk stand out due to their exceptional quality, fine texture, natural sheen, and high market value. These qualities have led to their widespread popularity in the textile industry and cultural heritage sectors. Given their superior attributes and commercial importance, the present review focuses primarily on these two silkworm species—Bombyx mori and Antheraea assamensis with the objective of unraveling the chemical and molecular mechanisms that underlie their feeding behavior and host plant interactions.

Although advances have been made in understanding the ecological and physiological aspects of silkworm–host plant relationships, the deeper molecular mechanisms, especially those linked to chemoreception, receptor gene expression, and downstream signaling remain incompletely understood. This review seeks to bridge this knowledge gap by compiling and analyzing current findings on the chemical ecology and molecular biology of silkworm feeding, with special emphasis on gustatory receptor functions, secondary plant metabolites, and genetic determinants that shape host specificity and adaptability in B. mori and A. assamensis.

### ****HOST PLANTS OF MULBERRY SILKWORM****

The domesticated silkworm, Bombyx mori L., is a phytophagous insect of significant economic importance, primarily reared for silk production. Although it is traditionally viewed as a monophagous species due to its strong preference for mulberry (Morus spp.) leaves, which provide a complete nutritional profile essential for its growth, development, and cocoon formation (Fraenkel, 1959), its feeding behavior is more accurately described as oligophagous. In addition to mulberry, B. mori has been experimentally observed to accept leaves from other plant families, including Ulmaceae (e.g., wild elm), Compositae (e.g., lettuce and dandelion), and Urticaceae (Fraenkel, 1959; Ishikawa *et al.,* 1969). However, these alternative host plants are markedly inferior in nutritional quality compared to mulberry, often resulting in poor larval development, reduced silk production, or even mortality due to phytochemical incompatibility or toxicity (Fraenkel *et al.,* 1959). Historical and comparative analyses (Zhang et al., 2013; Legay, 1958; Fraenkel, 1959; Jacobson, 2019) also support the classification of B. mori as an oligophagous insect, with restricted but observable feeding flexibility beyond the Moraceae family. Nonetheless, under practical rearing conditions, mulberry remains the only viable and nutritionally optimal host plant for sustainable and profitable silkworm cultivation.

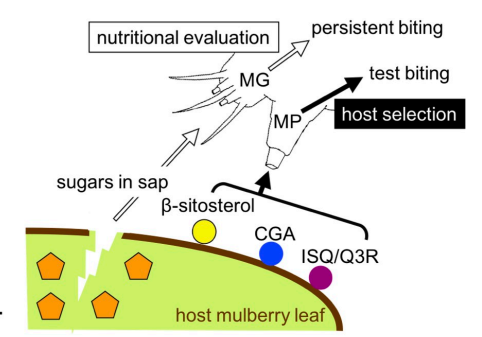
## ****CHEMOSENSORY MECHANISMS IN SILKWORM FEEDING BEHAVIOR****

Silkworm feeding behavior is orchestrated by a complex interplay of behavioral, physiological, and molecular mechanisms involving specialized chemosensory organs. Both Bombyx mori (the monophagous mulberry silkworm) and Antheraea assamensis (the polyphagous muga silkworm) rely on finely tuned sensory systems to recognize and discriminate among host plants, though their degree of selectivity and sensory adaptations differ considerably. Understanding these mechanisms is critical not only for elucidating silkworm–plant interactions but also for advancing sericultural practices, artificial diet development, and host plant improvement.

### ****3.1 Behavioral and Electrophysiological Basis of Host Recognition****

Initial host plant recognition in silkworms begins with long-range olfactory cues detected by chemoreceptors located on the antennae and maxillary palps (Sato & Touhara, 2008; Hansson, 1995; Johnson *et al.,* 2011; Nissan *et al.,* 2009). These cues, often in the form of plant-emitted volatile organic compounds, guide larvae to potential food sources (Ishikawa *et al.,* 1969). Upon contact, tactile and gustatory cues dominate, with test biting behavior serving as a crucial evaluative step (Van & Carlson, 2006). This is mediated by gustatory receptors located on the maxillary galea and labrum, which sense surface phytochemicals and exuded sap from host leaves (Bernays & Chapman, 1994, 2001; Watanabe, 1958; Watanabe *et al.,* 2011; Miles *et al., 2005;* Van & Schoonhoven, 1999) (Fig. 1).

Electrophysiological studies in B. mori have demonstrated that the larvae respond selectively to specific host-derived compounds, such as chlorogenic acid, β-sitosterol, and flavonoids like isoquercetin, found in Morus spp. leaves (Ito & Tanaka, 1959; Nayar & Fraenkel, 1962). Activation of sensory neurons upon detection of these compounds initiates feeding. Similar behavior has been observed in A. assamensis, though the range of acceptable host plants is broader, and the spectrum of responsive compounds is more diverse due to its polyphagous nature (**Mech & Vijay**, 2022; Haloi *et al.,* 2023).



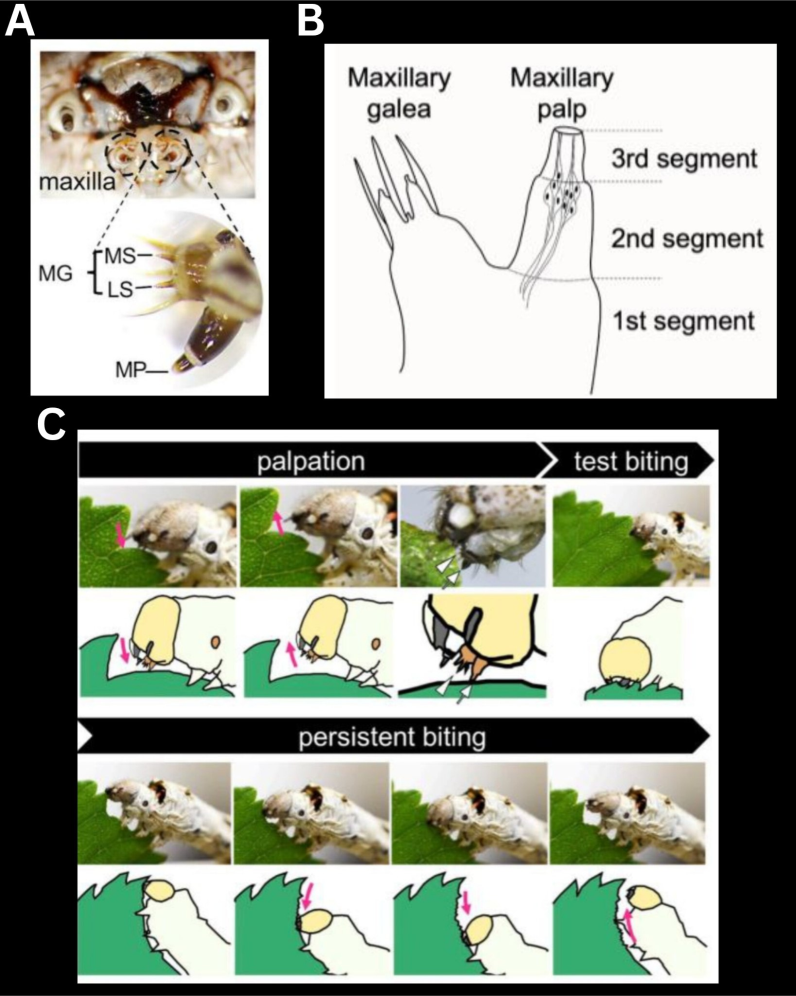
**Fig. 1. Host recognition and acceptance by *B. mori***

(Tsuneto *et al.,* 2020)

### ****3.2 Two-Factor Host Acceptance Model in**** Bombyx mori

Recent advances have clarified the two-step chemosensory mechanism in B. mori, as proposed by Tsuneto *et al.* (2020) (Fig.2). In this model, host acceptance involves sequential input from two key maxillary structures:

* The **maxillary palp (MP)** plays a critical role in the initial recognition phase. It houses ultra-sensitive gustatory neurons capable of detecting host-specific phytochemicals, including **chlorogenic acid, β-sitosterol, and isoquercetin**, at extremely low concentrations (attomolar to femtomolar levels). These compounds are found on the leaf surface waxes of mulberry and serve as reliable chemical signatures for B. mori. Activation of MP receptors by these molecules triggers the larva to engage in test biting behavior.
* Following this, the **maxillary galea (MG)** becomes active during the test bite stage, where it evaluates compounds released from the leaf sap. Sugars like **sucrose** and **myo-inositol,** which leak from the damaged plant tissues, act as feeding stimulants when detected by MG receptors (Ishikawa *et al.,* 1969; Wanner & Robertson, 2009). The detection of these compounds confirms the palatability and nutritional suitability of the plant, prompting the larva to initiate persistent feeding.



**Fig. 2. Sequential Feeding Behavior in Bombyx mori Larvae Mediated by Maxillary palp (MP) and Maxillary galea (MG). (A) Mouthparts of a silkworm larva. The maxilla consists of the MG and MP. The MG has 2 gustatory sensilla, the lateral styloconic sensillum (LS) and median styloconic sensillum (MS). (B) Schematic diagram of the maxilla of a silkworm larva. (C) Feeding on mulberry leaves by silkworm larvae. (1) Palpation: a silkworm larva first palpates the leaf surface with its maxilla (MP and MG) for 5–30 seconds. The white arrow and arrowhead indicate MP and MG. (2) Test biting: the larva bites the leaf edge several times intermittently during palpation. (3) Persistent biting: the larva nibbles the leaf edge repeatedly (2–3 times per second) with its head moving in the dorsoventral direction along the leaf edge. Magenta arrows indicate the direction of head movement.**

(Tsuneto *et al.,* 2020; Endo *et al.,* 2024)

## KEY PHYTOCHEMICALS INFLUENCING SILKWORM FEEDING

The feeding behavior of silkworms, particularly Bombyx mori and Antheraea assamensis, is primarily governed by a complex interaction between phytochemicals present on the leaf surface and within the sap. These compounds function either as stimulants or deterrents, modulating silkworm host plant selection, feeding initiation, and continuation. The maxillary palp (MP) and maxillary galea (MG) of silkworm house specialized gustatory receptors that detect these compounds and trigger appropriate behavioral responses (Ishikawa *et al.,* 1969; Endo *et al.,* 2024).

### 4.1 Feeding Stimulants

#### 4.1.1 Chlorogenic Acid

Chlorogenic acid has been consistently identified as one of the most effective feeding stimulants in B. mori. It acts during the palpation and test biting phase and is detected by sensory neurons in the MP. Endo *et al.* (2024) demonstrated that chlorogenic acid, when applied at attomolar concentrations, is sufficient to elicit test biting. Earlier work by Ito & Tanaka (1959) confirmed its bioactivity even in isolation from the leaf matrix and also reported strong feeding stimulation in response to chlorogenic acid extracted from mulberry leaves, linking its presence to increased larval acceptability.

#### 4.1.2 β-Sitosterol and Quercetin Glycosides

These phytochemicals also play a critical role in feeding initiation. β-Sitosterol and quercetin glycosides, often co-occurring with chlorogenic acid, significantly increase test biting frequency (Endo *et al.,* 2024; Tsuneto *et al.,* 2020; Chun, 1972; Devitt & Smith, 1985). According to behavioral assays, their combined presence triggers a greater than 50% acceptance rate in larvae during initial inspection (Endo *et al.,* 2024). These compounds may also act as leaf surface recognition cues, mimicking essential sterols and flavonoids needed for larval development.

#### 4.1.3 Sucrose and Myo-Inositol

Post-test biting, silkworm larvae evaluate internal sap for sugars that signal nutritional adequacy. Two specific gustatory receptors in the MG, BmGr6, which responds to sucrose, and BmGr9, which responds to myo-inositol, mediate this response (Endo *et al.,* 2024; Morinaga *et al.,* 2022). This receptor activation leads to persistent biting, a hallmark of host acceptance (Chun, 1972; Devitt & Smith, 1985). Nayar & Fraenkel (1962) similarly observed that sucrose solutions directly applied to leaf tissue increased biting frequency and reduced hesitation time. In A. assamensis, although receptor-specific data are limited, similar sugars and polyols in som (Persea bombycina) and soalu (Litsea monopetala) sap are believed to contribute to host plant recognition (Haloi *et al.,* 2023).

### 4.2 Feeding Deterrents

#### 4.2.1 Antagonistic Compounds in Non-Host Plants

Compounds found in non-host plants such as Artemisia vulgaris have been shown to interfere with gustatory signaling. Ethanol extracts of A. vulgaris suppressed sucrose-induced activation in MG neurons, reducing the likelihood of persistent biting (Endo *et al.,* 2024). This is consistent with findings by Xu *et al.* (2024), who demonstrated that sesquiterpene lactones and alkaloids in bitter plants could block sugar receptor pathways.

#### 4.2.2 Absence of Key Stimulants

Another form of deterrence is passive rejection, when test biting fails to yield sufficient levels of phagostimulants like chlorogenic acid, β-sitosterol, or sugars. Endo *et al.* (2024) noted that leaves lacking these three signature compounds triggered minimal feeding behavior. This explains why B. mori, though oligophagous, exhibits near-monophagous behavior under natural conditions.

## MOLECULAR GENETICS OF HOST PREFERENCE

## The host preference of the domesticated silkworm, Bombyx mori, presents a compelling model to explore the molecular genetic mechanisms underlying insect-plant interactions. As an oligophagous insect, B. mori feeds almost exclusively on mulberry (Morus spp.) leaves, despite having the capacity to accept a limited range of alternative host plants under artificial conditions. This narrow dietary preference is regulated not only by behavioral and physiological traits but also, and more importantly, by an intricate genetic network involving chemosensory receptors, particularly those governing gustatory and olfactory perception. With the advent of high-throughput molecular tools, including whole-genome sequencing, transcriptomic profiling, and gene-editing technologies, significant advances have been made in identifying key genes and pathways that shape the feeding specificity of B. mori.

#### 5.1 Gustatory System and Host Discrimination

The gustatory system plays a foundational role in host plant discrimination by enabling the silkworm to detect non-volatile compounds through specialized gustatory receptor neurons (GRNs) located on its maxillary galea. Electrophysiological investigations of the styloconic sensilla (SS-I and SS-II) revealed that these structures respond robustly to certain phagostimulants, especially vitamin C, sucrose, and inositol, which are abundant in mulberry leaves (Cui & Xu, 2001) (Table 1). Interestingly, these compounds can also exhibit mutual inhibitory effects on sensory neurons; for instance, vitamin C suppresses the response of SS-I to sucrose and inositol and vice versa, indicating a complex regulatory crosstalk between stimulatory and inhibitory signals at the peripheral sensory level.

At the molecular level, gustatory receptors (Grs), which belong to a distinct family of seven-transmembrane domain proteins, are central to decoding the chemical profile of potential food sources. Genome-wide annotations have identified up to 76 Gr genes in B. mori, several of which are expressed in chemosensory tissues such as the maxillae, antennae, and even in the central nervous system (Guo *et al.,* 2017). Among them, BmGr6, BmGr8, and BmGr4–10 function as sugar receptors, recognizing compounds like inositol and epi-inositol, which further reinforce mulberry specificity (Zhang *et al.,* 2011; Mang *et al.,* 2016). Notably, **the maxillary galea,** a critical gustatory organ—plays a fundamental role in assessing the nutritional quality of a leaf following **test biting**, the initial stage of feeding. Within this structure, **BmGr6 and BmGr9** serve as molecular sensors for sugars present in leaf sap, and their activation determines whether the larva proceeds to sustained feeding (Endo *et al.,* 2024). In contrast, BmGr53, BmGr16, BmGr18, and BmGr66 are categorized as bitter receptors, responding to deterrent compounds such as coumarin, caffeine, and pilocarpine (Kasubuchi *et al.,* 2018). These bitter Grs are critical for rejecting unsuitable or toxic plant material, adding another layer of selectivity to the silkworm’s feeding behavior.

Genetic studies have provided compelling evidence linking specific Gr genes to host preference. Using the CRISPR/Cas9 system, Baci *et al*. (2021) demonstrated that targeted disruption of the hestia gene converted B. mori from an oligophagous insect to one capable of consuming alternative foods such as apple and corn. Similarly, Zhang *et al.* (2019) reported that knockout of the bitter receptor gene Gr66 resulted in silkworm larvae that readily accepted atypical food sources, losing their inherent selectivity for mulberry. These findings underscore the genetic control of feeding preference and suggest that specific Grs function as molecular gatekeepers in host recognition.

#### 5.2 Olfactory Contributions to Feeding Behavior

In parallel with gustation, the olfactory system plays a critical role in long-range host detection. Located on the antennae, the olfactory apparatus includes odorant receptors (Ors), odorant-binding proteins (OBPs), and odorant-degrading enzymes (ODEs). These components work in concert to detect, transduce, and terminate responses to volatile semiochemicals released by host plants.

Odorant-binding proteins serve as the first interface between environmental volatiles and neuronal receptors. Gong *et al*. (2009) demonstrated that proteins such as GOBP, ABP, and PBPs (PBP1–3) are differentially expressed in the olfactory tissues of B. mori and are involved in transporting volatile molecules through the sensillar lymph to their corresponding Ors. Among these, PBP1 binds sex pheromones like bombykol and bombykal and transfers them to BmOr1 and BmOr3, respectively, facilitating not only mating behavior but also feeding-related responses.

Olfactory receptors themselves play a direct role in modulating feeding. For instance, BmOr56 has been shown to exhibit high sensitivity to cis-jasmone, a potent attractant in mulberry leaves, and mediates behavioral attraction in larvae (Tanaka *et al.,* 2009). Xin & Zhang (2020) further demonstrated that BmOr54 and BmOr56 exert opposing effects on feeding, Or56 promotes feeding while Or54 suppresses it. Simultaneous disruption of both genes using CRISPR/Cas9 significantly altered larval feeding patterns, establishing these genes as key regulators of olfactory-driven host selection.

The co-receptor Orco, essential for functional olfactory signaling complexes, is also implicated in feeding regulation. Sun *et al.* (2022) observed that Orco expression correlates with feeding intensity and is downregulated under starvation, suggesting that it contributes to olfactory sensitivity and, by extension, feeding behavior. Supporting this, odorant-degrading enzymes such as BmGSTD1 (a glutathione-S-transferase) and CYP6AE21 (a cytochrome P450) act to rapidly degrade odorant molecules after signal transduction, maintaining olfactory acuity and preventing sensory desensitization (Liu *et al.,* 2024; Wang *et al.,* 2011).

#### 5.3 Evolutionary Implications and Genomic Architecture

Comparative genomic analyses reveal that the chemosensory genes involved in host preference have undergone significant duplication and divergence. Zhang *et al.* (2011) noted that many Gr and Or genes are arranged in tandem on the same chromosomes, particularly chromosomes 7 and 17, implying evolutionary expansion through gene duplication events. These genes are believed to have originated from common ancestral loci and diversified to enable species-specific adaptation. Notably, Gr66 and its homologs appear to play pivotal roles in maintaining mulberry specificity, whereas mutations in these genes result in expanded dietary flexibility, suggesting a strong link between genotype and host preference phenotype.

**Table 1. Factors influencing feeding behavior in *B. mori***

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Classification** | **Silkworm-related and general functions** | **Factors** | **Function** | **Reference** |
| **Gustatory** | Styloconic sensilla on the maxillary galea (SSI and SSII) | Vitamin C, sucrose and inositol | SSI and SSII are the primary sensory sites initiating feeding. Vitamin C suppress their response of SSI to sucrose and inositol. Conversely, sucrose and inositol can inhibit the response of SS-I and SS-II to vitamin C. | Cui & Xu, 2001 |
|  | Gustatory receptors (Grs)- involved in food preference and selection | BmGr9, BmGr8, BmGr4-10, | Function as Sugar receptor | Mang *et al.,* 2016; Zhang *et al.,* 2011 |
|  |  | BmGr53, BmGr16, BmGr18, BmGr66 | Function as Bitter receptor | Zhang *et al.,* 2011; Kasubuchi *et al.,* 2018; Zhang *et al.*, 2019 |
| **Olfactory** | Odorant binding proteins (OBPs)- facilitate transport of odor molecules to sensory neurons, triggering signal transmission | GOBP | Capable of binding a range of odor molecules from food and the environment | Zhang, 2009 |
|  | Olfactory receptors (Ors)- convert odorant chemical signals into electrical responses via ion channel changes | BmOr56 | Highly responsive to cis-jasmone, a strong attractant from mulberry leaves; mediates behavioral attraction. | Tanaka *et al.,* 2009 |
|  |  | BmOr54 and BmOr56 | Or56 stimulates feeding, whereas Or54 suppresses it. These two receptors work antagonistically to regulate larval feeding | Liu, 2017 |
| **Mulberry leaf** | Attracting factors | α, β-hexenal, β, γ-hexenol, citral, linalyl acetate and linalol | Elicit feeding behavior in larvae | Watanabe *et al.,* 1958; Hamamura and Naito, 1961 |
|  | Biting factors | β-sitosterol | |  | | --- | |  |  |  | | --- | | Induces biting activity | | Takeda & Ueda, 1984; Nagata *et al.,*2011 |
|  | Swallowing factors | Cellulose, phosphate and silica, Sucrose, inositol, high levels of casein and ascorbic acid isoquercetin, morin, quercetin, chlorogenic acid, vanillin, polyphenolic acid, choline, certain vegetable oils and fatty acids | Enhance feeding and swallowing responses | Nagata *et al.,*2011; Song *et al.,* 2022; Naito et al., 1965; Kato and Yamada, 1966; Hamamura et al., 1966; Hayashiya, 1965 |
|  | Inhibitory factors | Tartaric acid, malic acid, sorbic acid, acetic acid and phosphoric acid | Suppress the growth and feeding of silkworms. | Tsai et al., 1978; Cui et al., 1998 |
|  | Avoidance factor | Artemisinin | Suppresses feeding behavior in larvae | Zhang, 2012 |

(Song *et al.,* 2021)

### 6. INSIGHTS FROM MUGA SILKWORM (ANTHERAEA ASSAMENSIS)

#### 6.1 Feeding Preferences and Host Plants

The golden-hued muga silk is produced by the semi-domesticated silkworm Antheraea assamensis Helfer, a polyphagous lepidopteran species known for its ability to utilize a diverse array of host plants. The natural distribution of its food plants spans extensively across the northeastern region of India, particularly in states such as Assam, Meghalaya, Manipur, Mizoram, Nagaland, Tripura, and Sikkim. Additionally, several northern and eastern states, including Himachal Pradesh, Uttarakhand, Uttar Pradesh, Gujarat, West Bengal, and the Union Territory of Puducherry, also support the growth of these host plants. In Arunachal Pradesh, their occurrence is more sporadic (**Mech & Vijay**, 2022; Haloi *et al.,* 2023).

Among the various host species, Persea bombycina (locally known as som) and Litsea monopetala (soalu) are regarded as the primary food plants, providing optimal nutrition and supporting healthy larval growth. Secondary host plants include Litsea salicifolia (dighloti) and Litsea citrata (mejankori), which are also commonly used but are considered slightly inferior in nutritional quality. Beyond these, several additional species serve as minor or tertiary hosts, including Cinnamomum glaucescens, Actinodaphne obovata, Michelia champaca, Zizyphus jujuba, Zanthoxylum rhetsa, and Celastrus monosperma (Neog *et al.,* 2005). These alternative hosts, although not commonly used in commercial rearing, can support larval development under specific ecological or seasonal constraints. A comprehensive list of host plants for A. assamensis is detailed in Table 2, highlighting the species' broad polyphagous feeding nature and adaptability to varied ecological conditions.

**Table 2. Host plants of muga silkworm**

|  |  |  |
| --- | --- | --- |
| **Status of Food Plant** | **Host Plants** | **Family** |
| **Primary** | *Persea bombycina* | Lauraceae |
|  | *Litsea monopetala* | Lauraceae |
| **Secondary** | *Cinnamomum camphora* | Lauraceae |
|  | *Cinnamomum tamala* | Lauraceae |
|  | *Litsea citrata* | Lauraceae |
|  | *Litsea salicifolia* | Lauraceae |
|  | *Actinodaphne augustifolia* | Lauraceae |
|  | *Actinodaphne obovata* | Lauraceae |
|  | *Celastrus monosperma* | Celastraceae |
| **Tertiary** | *Cinnamomum cecidodaphne* | Lauraceae |
|  | *Cinnamomum glanduliferum* | Lauraceae |
|  | *Cinnamomum obtusifolium* | Lauraceae |
|  | *Gmelina arborea* | Verbenaceae |
|  | *Litsea nitida* | Lauraceae |
|  | *Machilus odoratissima* | Lauraceae |
|  | *Magnolia pterocarpa* | Magnoliaceae |
|  | *Michelia champaca* | Magnoliaceae |
|  | *Michelia oblonga* | Magnoliaceae |
|  | *Symplocos grandiflora* | Symplocaceae |
|  | *Symplocos paniculata* | Symplocaceae |
|  | *Symplocos ramosissima* | Symplocaceae |

(Tikader *et al.,* 2013; Das *et al.,* 2020)

The muga silkworm, Antheraea assamensis, is a polyphagous insect that exhibits strong feeding preferences for members of the Lauraceae family, primarily Persea bombycina, Litsea polyantha, and Litsea citrata. Among these, the tender leaves of Litsea polyantha showed the highest concentration of soluble protein (17.17 mg/g), whereas the tender leaves of Persea bombycina recorded the highest total phenol content (119.79 mg/100g) (Table 3). In contrast, the mature and medium leaves of Litsea citrata exhibited the lowest levels of soluble protein (8.86 mg/g) and total phenols (15.50 mg/100g), which contribute to both nutritional quality and chemical signaling essential for larval development (Haloi *et al.,* 2023; Neog *et al.,* 2005).

**Table 3. Comparative Analysis of Protein, Phenolic Content, and PAL Activity in Leaves of Host Plants at Different Maturity Stages**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Host Plant** | **Maturity Level** | **Protein Content (mg/g)** | **Total Phenol Content (mg/100g)** | **PAL Activity (nmole/mg/min)** |
| *Persea bombycina* | Tender | 16.23 | 119.79 | 3.48 |
| Medium | 11.61 | 47.26 | 4.14 |
| Mature | 9.98 | 53.12 | 2.06 |
| *Litsea polyantha* | Tender | 17.17 | 40.41 | 3.03 |
| Medium | 13.67 | 101.39 | 3.22 |
| Mature | 11.19 | 34.30 | 1.44 |
| *Litsea salicifolia* | Tender | 14.23 | 31.10 | 2.54 |
| Medium | 13.03 | 47.51 | 2.42 |
| Mature | 9.44 | 101.97 | 1.19 |
| *Litsea citrata* | Tender | 12.13 | 34.51 | 2.52 |
| Medium | 9.93 | 15.50 | 1.81 |
| Mature | 8.86 | 28.43 | 0.96 |

(Neog *et al.,* 2011 b)

#### 6.2 Role of Chemical Stimulants

Feeding stimulation in A. assamensis is driven by an array of phytochemicals. Flavonoids such as myricetin and 7,2’,4’-trimethoxy-dihydroxy flavone, along with β-sitosterol (0.69–1.06 %), are crucial in eliciting biting and acceptance behaviors. Additionally, volatile terpenoids like caryophyllene and linalyl acetate, detected via olfactory pathways act as attractants that guide larvae toward suitable foliage. These chemicals, often concentrated in younger leaves, serve as both feeding cues and developmental enhancers (**Mech & Vijay**, 2022; Tikader *et al.,* 2013).

#### 6.3 Secondary Metabolite Analysis

High-performance liquid chromatography (HPLC) profiling of P. bombycina leaves has revealed high concentrations of chlorogenic acid (1.45–2.06 %) and β-sitosterol in tender and semi-mature stages, which contribute to palatability and possess antioxidant and antimicrobial properties. Such compounds play a significant role not only in stimulating larval feeding but also in enhancing cocoon quality and larval immunity (Das *et al.,* 2020; Tikader *et al.,* 2013) (Table 4).

**Table 4. Quantitative Profiling of Secondary Metabolites and Phenolic Compounds in Persea bombycina Leaves at Different Maturity Stages**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Sl. No.** | **Secondary Metabolites** | **Tender** | **Medium** | **Mature** |
| 1 | β-sitosterol (%) | 1.06 | 0.82 | 0.69 |
| 2 | Chlorogenic acid (%) | 1.81 | 2.06 | 1.45 |
| 3 | Phytic acid (mg/100g) | 83.33 | 1642.20 | 2310.05 |
| 4 | Total phenol (%) | 1.946 | 1.182 | 0.712 |
| 5 | Acid detergent fibre (%) | 16.90 | 23.35 | 26.50 |
| 6 | Acid detergent lignin (%) | 8.02 | 13.52 | 15.83 |
| 7 | Tannin (%) | 6.71 | 2.05 | 3.00 |
| **Sl. No.** | **Phenolic Compound** | **Tender (g/100g)** | **Medium (g/100g)** | **Mature (g/100g)** |
| 1 | Quercetin | 0.008 | 0.015 | 0.025 |
| 2 | 3’, 4’ Dimethyl Quercetin | 0.026 | 0.035 | 0.042 |
| 3 | Morin | 0.028 | 0.035 | 0.045 |
| 4 | Myrecetin | 0.040 | 0.025 | 0.018 |
| 5 | 7, 2’, 4’ Trimethoxy dihydroxy flavone | 0.038 | 0.030 | 0.015 |
| 6 | 2’, 4’ Dimethyl Morin | 0.012 | 0.025 | 0.033 |

(Neog *et al.,* 2011a, b)

### ****6.4 Chemosensory Flexibility in**** Antheraea assamensis

In contrast to the strict selectivity of B. mori, A. assamensis displays remarkable chemosensory plasticity, which supports its polyphagous lifestyle. The larvae accept a broad spectrum of host plants, primarily from the Lauraceae family (Persea bombycina, Litsea monopetala), but also including secondary and tertiary hosts like Michelia champaca and Cinnamomum glaucescens (Tikader *et al.,* 2013; Das *et al.,* 2020) (Table 5). Although fewer electrophysiological studies have been conducted on A. assamensis, analogous research on Antheraea pernyi and Antheraea yamamai suggests the presence of a well-developed array of gustatory and olfactory receptor genes expressed in the maxillary organs, antennae, and palps (Jiang *et al.,* 2023; Li *et al.,* 2020).

Behaviorally, muga larvae also exhibit test biting followed by committed feeding, implying that a similar two-step chemosensory process may operate. However, the thresholds for stimulant detection are likely broader, and receptor tuning less specific, allowing the species to adapt to varying host chemical profiles. This sensory generalism is advantageous for survival in fluctuating environments where host plant availability changes seasonally.

Adult oviposition behavior in both species is chemically mediated. Females detect surface volatiles and cuticular compounds of leaves via chemoreceptors on the tarsi and ovipositor, ensuring eggs are laid on suitable host plants (Gothard *et al.,* 2005; Bossart & Scriber, 1999). In A. assamensis, the wider oviposition range corresponds with larval polyphagy, whereas in B. mori, oviposition is limited due to domestication and dependence on cultivated mulberry.

**Table 5. Behavioral Response of Muga Silkworm Larvae to Various Chemical Stimuli**

|  |  |  |  |
| --- | --- | --- | --- |
| **Sl. No.** | **Name of the Chemical** | **Attraction** | **Biting** |
| 1 | Myrcetin | No action | +ve |
| 2 | Morin | No action | No action |
| 3 | Quercetin | No action | No action |
| 4 | 7, 2′, 4′ Trimethoxy dihydroxy flavone | No action | +ve |
| 5 | 3′, 4′ Dimethyl Quercetin | No action | No action |
| 6 | 2′, 4′ Dimethyl Morin | No action | No action |
| 7 | Beta sitosterol | No action | +ve |
| 8 | Myrcetin+ Beta sitosterol | Highly +ve | Highly +ve |
| 9 | 7, 2′, 4′ Trimethoxy dihydroxy flavone +Beta sitosterol | Highly +ve | Highly +ve |
| 10 | Citral | +ve | -ve |
| 11 | Linalool | +ve | -ve |
| 12 | Linalyl Acetate | Highly +ve | -ve |
| 13 | Myrcetin+7, 2′, 4′ Trimethoxy dihydroxy flavone +Beta sitosterol | +ve | -ve |
| 14 | Geraniol | No action | No action |
| 15 | Hexanol | No action | No action |
| 16 | Caryophyllene | +ve | +ve |
| 17 | Decyl aldehyde | +ve | +ve |
| 18 | Dodecyl aldehyde | +ve | +ve |
| 19 | Geraniol+ Hexanol+ Caryophyllene | Highly +ve | Highly +ve |
| 20 | Gallic acid | -ve | +ve |
| 21 | Azainidole | -ve | Highly -ve |
| 22 | Control (water) | No action | No action |

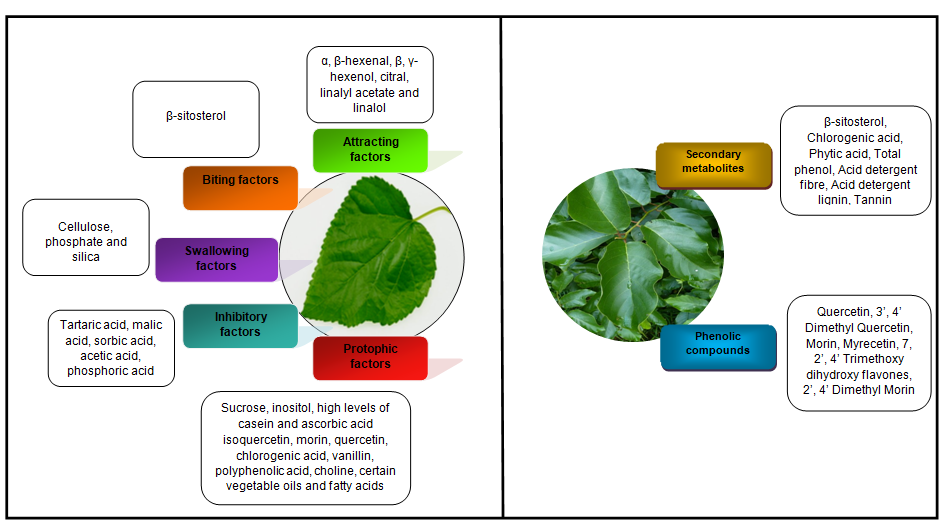
(Neog *et al.,* 2011 b)

1. **COMPARATIVE CHEMOSENSORY MECHANISMS UNDERLYING MONOPHAGY AND POLYPHAGY IN SILKWORMS**

The divergence in feeding strategies between Bombyx mori and Antheraea assamensis reflects their distinct evolutionary histories and varying degrees of domestication. B. mori, a fully domesticated lepidopteran, exhibits strict monophagy, feeding exclusively on mulberry (Morus spp.). This limited host range is driven by a highly specialized and genetically constrained chemosensory system. Gustatory receptors (Grs), particularly Gr66, play a critical role in selective host plant recognition, ensuring high host fidelity and restricting dietary flexibility (Zhang *et al.,* 2019).

In contrast, A. assamensis, the muga silkworm, exhibits polyphagous behavior, feeding on a variety of host plants within the Lauraceae family, including Persea bombycina, Litsea polyantha, and L. citrata. This broader host acceptance is facilitated by a more diverse and adaptable set of gustatory and olfactory receptors, allowing larvae to respond to a wide array of phytochemical cues. The species’ semi-domesticated status and its ecological association with diverse forest environments likely contribute to the maintenance of this chemosensory plasticity. While extensive research has elucidated the molecular mechanisms governing host recognition and feeding behavior in B. mori, such as the role of specific feeding stimulants like β-sitosterol, sucrose, chlorogenic acid, and volatile organic compounds, the corresponding mechanisms in A. assamensis remain poorly understood. The phytochemical composition of its primary host, Persea bombycina (Som), and its influence on larval feeding behavior has not been comprehensively investigated.

To bridge this knowledge gap, further studies are required to identify and functionally characterize the gustatory receptor (Gr) genes in A. assamensis. Comparative transcriptomic analyses, receptor-ligand interaction assays, and behavioral studies are essential to uncover the molecular and neuroethological basis of polyphagy in this species. Such research will not only advance fundamental understanding of host plant adaptation but also support practical applications in muga silkworm breeding, host plant selection, and artificial diet formulation. Overall, comparative insights into the chemosensory systems of monophagous and polyphagous silkworms can significantly inform strategies for sustainable sericulture, species conservation, and the management of host plant resources.



**Fig. 3. Comparative analysis of phytochemical feeding cues in mulberry (Morus spp.) and Som (Persea bombycina) leaves influencing silkworm behavior**

## 8. APPLICATIONS AND FUTURE DIRECTIONS

### 8.1 Artificial Diet Formulation

The elucidation of key phytochemical stimulants, such as chlorogenic acid, β-sitosterol, quercetin glycosides, and sugars like sucrose, paves the way for designing nutritionally and behaviorally effective artificial diets. By incorporating these compounds into synthetic feed matrices, researchers can significantly improve the palatability and acceptability of artificial diets, especially for B. mori, which traditionally exhibits reluctance toward non-mulberry feeds.

### 8.2 Silkworm Breeding and Genetic Engineering

Advancements in molecular biology and genome editing techniques (e.g., CRISPR-Cas9) provide new opportunities to manipulate gustatory receptor genes like Gr66, Gr6, and Gr9. Modifying these receptors could yield silkworm strains capable of feeding on alternative or less resource-intensive host plants, enhancing sustainability and adaptability under changing agro-ecological conditions.

### 8.3 Pest Management Strategies

The knowledge derived from silkworm host plant interactions can be extended to agricultural pest species. Understanding chemosensory mechanisms can help develop targeted pest deterrents or resistant crop varieties by manipulating surface chemistry or metabolic pathways involved in host recognition.

### 8.4 Future Research Directions

While considerable research has elucidated the molecular and chemical basis of feeding in Bombyx mori, there remains a substantial gap in our understanding of the equivalent mechanisms in Antheraea assamensis. Future research should prioritize the identification and functional characterization of gustatory and olfactory receptor genes in A. assamensis, as well as the downstream neural circuits involved in host plant selection. Comparative transcriptomic analyses between larval stages fed on different host plants could reveal regulatory networks that govern polyphagy.

Furthermore, behavioral assays combined with metabolomic profiling of host plants can help delineate the precise chemical cues guiding muga silkworm feeding behavior. Integration of these approaches with genome editing tools will be instrumental in developing improved silkworm strains and refining sericultural practices tailored to the unique biology of muga silkworms. These insights hold promise not only for sericulture improvement but also for broader applications in insect ecology, evolutionary biology, and integrated pest management.

**9. CONCLUSION**

Silkworm feeding behavior is driven by a complex integration of plant-derived phytochemicals, chemosensory detection, and genetic regulation. In *Bombyx mori*, feeding is highly specific to mulberry due to the action of gustatory receptors such as Gr66, Gr6, and Gr9. These receptors recognize stimulants like chlorogenic acid, β-sitosterol, and sugars, triggering a precise sequence of feeding behaviors. Gene editing studies have confirmed that these receptors are key determinants of host fidelity. In contrast, the polyphagous muga silkworm, *Antheraea assamensis*, responds to a broader array of phytochemicals including flavonoids and terpenoids from multiple Lauraceae host plants. While its feeding ecology is well-documented, the molecular basis of its host selection remains underexplored, highlighting a critical area for future investigation.

These insights not only illuminate evolutionary differences in host adaptation but also offer practical applications. Artificial diets incorporating identified stimulants can improve feed acceptance, while receptor-targeted genetic modifications may broaden host range. Additionally, this knowledge has implications for pest management and crop protection. Future research should focus on expanding molecular and functional studies in non-mulberry silkworms like *A. assamensis*, including receptor profiling and behavioral assays. Such efforts will support sustainable sericulture and advance our broader understanding of insect-plant interactions.

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