



International Journal of Agriculture and Food Science

ISSN Print: 2664-844X
 ISSN Online: 2664-8458
 NAAS Rating (2026): 4.97
 IJAFS 2026; 8(3): 294-303
www.agriculturaljournals.com
 Received: 02-01-2026
 Accepted: 04-02-2026

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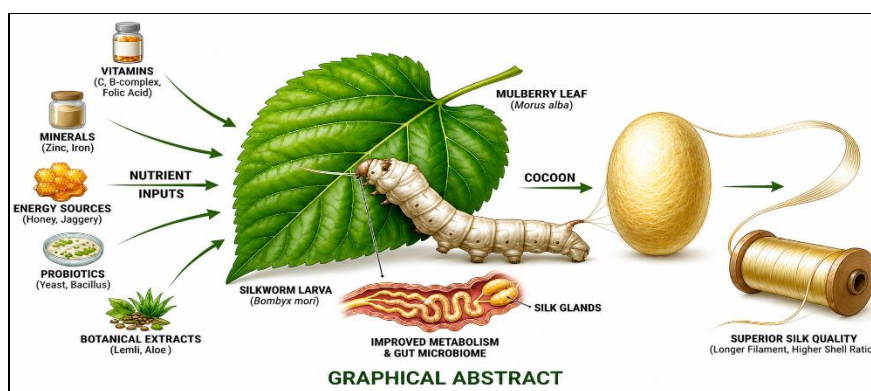
Silkworm nutrition and its impact on growth, cocoon yield and silk quality

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DOI: <https://www.doi.org/10.33545/2664844X.2026.v8.i3d.1263>

Abstract

Silkworm (*Bombyx mori* L.) nutrition represents a critical determinant of productivity and sustainability in sericulture, directly influencing larval growth, cocoon yield and silk quality. This review synthesizes current understanding of the nutritional requirements of *B. mori*, emphasizing the roles of macronutrients (proteins, carbohydrates, lipids), micronutrients (vitamins, minerals, sterols) and water in supporting metabolic processes, silk protein biosynthesis and immune function. Mulberry (*Morus* spp.) leaf quality shaped by genotype, seasonal variation, and agronomic practices emerges as the primary factor governing silkworm performance, with protein content, carbohydrate availability, moisture levels and mineral composition showing particularly strong correlations with commercial traits. We examine the biochemical composition of mulberry leaves across cultivars and seasons, documenting their effects on larval development, digestive efficiency and cocoon parameters. The review also evaluates artificial and semi-artificial diets as alternatives to mulberry feeding, analyzing their formulation principles, comparative performance, and current limitations including altered metabolism, reduced gut microbiota diversity and variable silk quality. Nutritional interventions including fortification with amino acids, vitamins, minerals, probiotics and bioactive compounds demonstrate substantial potential for enhancing cocoon weight, shell ratio, filament length and silk protein composition, though optimal dosages and application methods require careful calibration to avoid adverse effects. Besides, nutrition significantly modulates silkworm physiology by influencing growth rate, disease resistance and energy metabolism, with probiotic supplementation and micronutrient enrichment showing particular promise for improving larval health and pathogen tolerance. The integration of strategic genotype selection optimized agronomic management of mulberry, balanced nutritional supplementation and judicious use of artificial diets offers pathways toward more productive and climate-resilient sericulture systems. Future research priorities include refining nutrient combinations for different silkworm strains and developmental stages, developing cost-effective fortification strategies, improving artificial diet formulations to better approximate mulberry nutrition and aligning sericultural practices with principles of environmental sustainability and circular agriculture.



Keywords: *Bombyx mori*, mulberry nutrition, silk quality, cocoon yield, artificial diet, nutritional supplementation, sericulture

1. Introduction

The domesticated silkworm, *Bombyx mori* L., occupies a unique nexus of biology and rural economy: an insect whose life history and commercial value are tightly bound to a single food plant and to human-managed landscapes. As an essentially monophagous lepidopteran,

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B. mori depends almost entirely on mulberry (*Morus* spp.) foliage during its larval stages; consequently, any attempt to improve silk yield must start with a clear account of the leaf as both substrate and nutrients cape. Mulberry leaf quality is not a static property but a multidimensional, context-dependent trait shaped by cultivar genetics, edaphic fertility, climate and agronomic regime. This variability matters because the mulberry leaf biochemical portfolio proportions of carbohydrates, proteins and free amino acids, lipids, micronutrients and vitamins maps directly onto the silkworm metabolic economy, governing everything from energy allocation and silk protein synthesis to immune competence. When the plant fails to meet the insect's nutritional demands, the phenotypic consequences are predictable and consequential lowered feed conversion efficiency, lighter cocoons and shells, and greater disease susceptibility. These patterns have been documented across recent studies. (Sudha *et al.* 2023, Aramani *et al.* 2025, Bora *et al.* 2024, Kruthika *et al.* 2025)^[97, 4, 13, 50].

Contemporary work underscores that improvements in sericultural performance rarely follow from single, blunt intervention rather, gains emerge where genotype, diet and management are aligned. Selecting silkworm strains with superior nutrient-use efficiency and feeding them with nutrient-dense mulberry varieties produces consistent improvements in economically relevant traits across different voltinism groups (Borah & Boro, 2020, Kamate *et al.* 2010)^[15, 41]. Equally important, the relationships among nutrients are often non-additive: the balance of amino acids can modulate protein assimilation, carbohydrates influence silk gland activity and micronutrients shape both enzymatic processes and disease resistance. In practical terms, this means that optimizing silk production is a multidimensional problem one that requires attention to stoichiometry and trade-offs (for example, accelerated larval growth versus maintenance of robust immune function), rather than simple maximization of any single dietary component.

Against this background, two parallel strategies have received most attention: fortifying mulberry foliage and developing complementary or artificial feeding regimes. Experimental supplementation with amino acids, vitamins, minerals, probiotics and proteinaceous additives such as spermidine, egg albumen, honey and glucose has repeatedly improved larval weight, silk gland development, cocoon quality and pathogen resilience in controlled trials (Rajan *et al.* 2021, Borgohain, 2015, Aramani *et al.* 2025, Nath *et al.* 2025, Bora *et al.* 2024, Moustafa, 2024)^[83, 16, 4, 74, 13, 69]. These results are promising, yet they also expose a cautionary boundary: over-fortification or nutrient imbalance can undermine silk quality or larval health. Artificial and semi-artificial diets offer an attractive technological alternative in regions where mulberry is scarce or seasonal, but economic feasibility and variable field performance especially under heterogeneous rearing conditions have so far constrained widespread adoption (Bhattacharyya *et al.* 2016)^[8]. In other words, technical potential is necessary but not sufficient, social and economic contexts, alongside ecological variability, determine whether an innovation translates into sustained yield gains for farmers.

The research these days is therefore converging on integrative solutions: identifying optimal nutrient combinations rather than single magic additives, synchronizing soil, foliar and cultivar choices to produce

climate-resilient, nutrient-stable mulberry stands, and embedding sericulture within broader sustainability principles that recognize trade-offs at the agroecosystem scale (Thulasi & Sivaprasad, 2015, Sudha *et al.* 2023, Kruthika *et al.* 2025)^[103, 97, 50]. This review synthesizes those strands the physiological demands of *B. mori*, the biochemistry and management of mulberry foliage, the promise and pitfalls of artificial diets and the downstream effects of nutrition on cocoon yield, silk properties and silkworm physiology with the explicit aim of moving beyond descriptive accounts toward actionable, evidence-based nutritional strategies that are sensitive to agronomic realities and farmer livelihoods.

1.1 Nutritional Requirements of Silkworms

1.1.1 Macronutrients (proteins, carbohydrates, lipids)

a. Proteins

Among macronutrients governing silkworm growth and productivity, dietary protein occupies a central functional role, serving not only as a structural nutrient but also as the direct biochemical precursor of silk. In *Bombyx mori*, proteins derived almost exclusively from mulberry leaves are assimilated into metabolic enzymes, somatic tissues, and most critically, the hypertrophied silk glands responsible for fibroin and sericin synthesis. Mulberry foliage typically contains nearly 27% crude protein; however, marked cultivar-dependent variation exists, with genotypes such as Ichinose and Kayrio Nezumigaeshi consistently exhibiting higher protein content and superior feeding value (Raghuvanshi *et al.* 2019, Jat *et al.* 2010)^[80, 39]. Enhanced protein availability is closely associated with increases in larval weight, cocoon and shell weight, shell ratio and filament length, reflecting the efficient conversion of dietary nitrogen into silk proteins during the final larval instars (Matei *et al.* 2006, Bothikar *et al.* 2014, Mala and Vijila, 2017)^[66, 17, 60]. Nevertheless, protein utilization is strongly influenced by leaf freshness, feeding frequency and the metabolic support provided by carbohydrates and lipids, which supply the energy required for effective protein assimilation and silk gland activity. Consequently, improvements in mulberry nutritional management through cultivar selection, soil fertility enhancement, and optimal harvest timing often yield greater productivity gains than protein supplementation alone (Raghuvanshi *et al.* 2019, Rajabov *et al.* 2023)^[39, 82]. While protein sufficiency is indispensable, optimal silkworm performance ultimately depends on balanced nutrition, as excessive or poorly synchronized protein intake may reduce metabolic efficiency unless supported by adequate energy substrates, micronutrients, favorable rearing conditions, and effective disease management (Pavankumar *et al.*, 2020, Thirumalaisamy *et al.*, 2009)^[77, 102].

b. Carbohydrates

Carbohydrates constitute the primary energy source sustaining rapid larval growth and the intense biosynthetic demands of silk production in *Bombyx mori*. Supplied almost entirely by mulberry leaves, which typically contain around 11% carbohydrates, these compounds support ATP-intensive metabolic processes, particularly within the silk glands where silk protein synthesis occurs (Kavitha *et al.* 2014)^[43]. During later developmental stages, carbohydrate substrates are routed through interconnected glycolytic, oxidative and gluconeogenic pathways to meet the changing

energetic requirements of metamorphosis (Raghuvanshi *et al.* 2019)^[80]. Carbohydrate availability varies significantly among mulberry genotypes, and cultivars with higher soluble carbohydrate content, such as *Morus nigra*, consistently promote improved larval growth, cocoon weight, shell ratio and filament quality (Abdelmegeed, 2016, Srivastava and Elangovan, 2011)^[1, 95]. These responses are further influenced by feeding frequency and leaf freshness, which together regulate carbohydrate intake efficiency and metabolic utilization (Prasad and Madhavi, 2020, Marin *et al.* 2022)^[78, 64]. Supplementary inputs, including micronutrients and readily metabolizable additives such as honey, have been shown to enhance carbohydrate assimilation and energy metabolism, particularly under conditions of suboptimal leaf quality (Raghuvanshi *et al.* 2019, Kumari *et al.* 2011)^[80, 55]. However, the productive contribution of carbohydrates to silk yield is closely dependent on their metabolic integration with proteins and other nutrients, reinforcing the importance of balanced feeding strategies for sustained improvements in sericultural performance.

c. Lipids

Although present in smaller quantities than proteins and carbohydrates, lipids play a critical role in regulating physiological stability and developmental success in *Bombyx mori*. Lipids and essential fatty acids derived from mulberry leaves contribute to membrane integrity, enzyme modulation, endocrine regulation, and energy buffering, functions that become particularly important during late larval stages and metamorphosis (Habeanu *et al.* 2023, Hiremath *et al.* 2009)^[34, 35]. Inadequate lipid availability can adversely affect pupal transformation, immune competence, and cocoon formation, underscoring the sensitivity of these processes to lipid nutrition (Kochi and Kaliwal, 2006)^[48]. The lipid content of mulberry foliage is influenced by agronomic practices, with organic fertilizers, biofertilizers and compost amendments shown to enhance leaf lipid profiles and subsequent lipid deposition in silkworm tissues, including larvae, pupae, and reproductive stages (Agnihotri *et al.* 2015)^[2]. Mineral nutrition further modulates lipid metabolism, as trace elements such as zinc act as enzymatic cofactors involved in lipid synthesis and transport, thereby supporting larval growth efficiency and cocoon yield (Agnihotri *et al.* 2015, Kumar *et al.* 2015)^[2, 55]. However, the functional benefits of lipids are realized only when balanced with adequate protein and carbohydrate supply, as disproportionate lipid enrichment may disrupt metabolic equilibrium. Thus, lipid nutrition reinforces the broader principle that integrated mulberry nutrient management, rather than single-nutrient enhancement, is essential for sustained gains in silk productivity.

1.1.2 Micronutrients (vitamins, minerals, sterols)

Beyond macronutrients, micronutrients play a critical regulatory role in the physiology, development, and silk-producing efficiency of *Bombyx mori*. Vitamins, minerals and sterols supplied through mulberry leaves function mainly as enzymatic cofactors and structural regulators, influencing metabolic pathways, hormone-controlled molting and the regulation of silk biosynthesis. Although mulberry foliage provides a baseline supply of micronutrients, several studies indicate that targeted supplementation can enhance economically important traits

without altering the basic feeding regime. Among minerals, zinc is particularly important, acting as a cofactor in protein, lipid and carbohydrate metabolism, shortening larval and pupal duration, and improving fecundity and cocoon quality (Wani *et al.* 2018)^[106]. Calcium, potassium, magnesium and phosphorus further support silk gland activity and fibroin synthesis, strengthening overall silk output (Raghuvanshi *et al.* 2019)^[80].

Vitamins and sterols exert equally significant effects on silkworm performance. Pyridoxine (vitamin B₆) enhances amino acid metabolism and enzymatic efficiency, leading to improved larval growth and cocoon traits when administered through fortified leaves (Borah and Boro, 2018)^[15]. Sterols are indispensable because silkworms lack the ability to synthesize them endogenously and depend entirely on dietary sources; cholesterol and sterols such as 5 α -cholest-6-en-3 β -ol effectively support growth and molting, whereas structurally similar sterols may be metabolically inadequate or disruptive (Kumar *et al.* 2017, Ruth *et al.* 2019)^[63, 89]. Conventional mineral supplementation using salts such as ZnSO₄, FeSO₄, and CuSO₄ enhances feeding efficiency, nutrient assimilation and silk gland development (Mamiya *et al.* 1989)^[61], while nano-formulations further improve bioavailability and physiological response (Chakrapani *et al.* 2022)^[18]. However, micronutrient inputs require careful optimization, as excessive or imbalanced supplementation can impair growth and prolong development, emphasizing the need for integration within a balanced nutritional framework.

1.1.3 Moisture requirements

Moisture availability is a vital yet often overlooked component of silkworm nutrition, strongly influencing the assimilation and metabolic utilization of dietary nutrients. In *Bombyx mori*, water intake occurs predominantly through mulberry leaves, whose high moisture content facilitates enzymatic digestion, nutrient solubilization, and transport across the midgut. Genotypic variation in leaf moisture content therefore has important biological implications, as mulberry cultivars with high relative water content reaching up to 98% consistently promote enhanced larval growth, metabolic efficiency, and cocoon quality by reducing physiological stress and improving digestive processes (Biradar, 2020, Borah and Boro, 2018)^[11, 15].

Silkworms also exhibit physiological adaptations to regulate internal water balance. Under restricted feeding conditions, larvae increase water retention efficiency to maintain hydration and silk gland function, highlighting the importance of adequate dietary moisture for metabolic stability and survival (Gencoglan and Baspinar, 2016)^[32]. Feeding management further influences hydration status, as frequent provision of fresh leaves ensures synchronized water and nutrient intake, while artificial diets require precise, stage-specific moisture regulation to prevent developmental disturbances (Delvi *et al.* 1988, Raghuvanshi *et al.* 2019)^[26, 80]. During metamorphosis, total body water content declines while lipid reserves increase, reflecting internal physiological reorganization rather than dehydration (Borah and Hazarika, 2019)^[14]. At the digestive level, dietary quality regulates midgut water transport through ion-mediated mechanisms, particularly involving potassium balance (Rahmathulla *et al.* 2006)^[81]. In addition, ambient temperature and humidity interact with dietary moisture to influence rearing performance, emphasizing that optimal

silk production depends on coordinated management of leaf quality, feeding practices and microclimatic conditions (Zerahn, 1985)^[110].

2. Mulberry Leaf Quality and Its Influence on Nutrition

2.1 Biochemical composition of mulberry leaves

The nutritional value of mulberry leaves in sericulture is primarily determined by their biochemical composition, which governs nutrient availability and physiological utilization by silkworms. This composition is highly variable, influenced by genotype and growing environment, and includes proteins, carbohydrates, pigments, vitamins, minerals and secondary metabolites that collectively define feeding quality. Protein content generally ranges from 15% to 35%, with elite cultivars such as V1 exhibiting exceptionally high soluble protein concentrations (up to 111.40 mg g⁻¹), providing a strong nitrogen source for silk gland development. Carbohydrate content also varies with genotype and leaf position; in TR-10, apical leaves accumulate higher sugar fractions that enhance energy supply during rapid larval growth (Bhat *et al.* 2022, Khyade and Sakdeo, 2012, Srivastava and Elangovan, 2011)^[7, 45, 95]. Variations in chlorophyll content among genotypes such as S13 and S1635 influence photosynthetic efficiency and assimilate production, while elevated proline levels in stress-tolerant varieties (*e.g.*, S164 and S13) indicate adaptive biochemical traits (Jyothi *et al.* 2014)^[40]. Mulberry leaves further supply β -carotene, ascorbic acid, and essential minerals including calcium, iron and potassium, supporting silkworm metabolism and immunity (Marin *et al.* 2023, Kumar and Chauhan, 2011)^[65, 52]. Leaf biochemistry responds strongly to agronomic interventions, as nitrogenous sprays and growth regulators enhance protein accumulation and micronutrient applications (zinc, copper, and iron) improve overall nutrient balance (Khakwani *et al.* 2022, Mahesh *et al.* 2017)^[44, 58], emphasizing the importance of integrated cultivar selection and management for optimal leaf quality.

2.2 Seasonal and varietal variations

Mulberry leaf nutritional quality is dynamic and shaped by interactions between genotype and season, with direct consequences for silkworm performance. Varietal differences establish inherent biochemical potential, as cultivars such as V1 consistently exhibit high soluble protein and free amino acid content, while S13, Chinese White, TG, and S1708 combine elevated protein and sugar levels that support improved larval growth and cocoon yield (Bhat *et al.* 2022, Bongale and Chaluvachari, 1993, Chaluvachari *et al.* 1997, Kim *et al.* 2001)^[7, 12, 19, 47]. Seasonal factors strongly modulate these varietal traits. Concentrations of protein, chlorophyll, and key minerals such as calcium and potassium often peak during mid-summer due to enhanced photosynthetic activity and nutrient assimilation (Chaluvachari *et al.* 1997, Kim *et al.* 2001)^[19, 47]. Harvest timing further influences leaf quality, with optimally harvested leaves showing higher crude protein and lower fiber content, improving digestibility and nutrient uptake (Murthy *et al.* 2013)^[71]. Protein-rich varieties such as Hikojiro and Shimanouchi consistently support higher cocoon production efficiency, while differences in leaf moisture content among genotypes affect digestive efficiency and nutrient absorption (Jyothi *et al.* 2014, Machii and Katagiri, 1991)^[40, 57], highlighting the

need to align varietal selection with seasonally optimized harvesting.

2.3 Effect on silkworm growth and development

Mulberry leaf quality plays a decisive role in regulating the growth and development of *Bombyx mori*, directly influencing larval performance, cocoon yield and silk quality through its effects on nutrient availability and metabolic efficiency. Variations in protein, carbohydrate, chlorophyll and proline content among mulberry genotypes significantly affect larval growth, with high-protein varieties such as S13 and Chinese White supporting superior development, while vitamins and minerals further enhance cocoon traits and physiological performance (Bhat *et al.* 2022, Ravikumar *et al.*, 2020)^[7, 88].

Mulberry management practices strongly influence these outcomes. Fertilization with urea, TSP and NPK improves leaf nutritional quality, increasing larval growth rate and food conversion efficiency (Tanjung, 2020)^[100]. High leaf moisture content promotes greater larval weight gain and cocoon weight by enhancing digestion and silk synthesis (Kamate *et al.* 2010)^[41], while organic manure application and environmental conditions further modulate nutritive value (Sharma *et al.* 2020, Sudha *et al.* 2023)^[94, 97]. However, excessive supplementation, including high doses of vitamin B₁ or certain plant-based disease-control treatments, can negatively affect larval growth (Manjunatha *et al.* 2017, Tanjung, 2022)^[101], underscoring the importance of balanced nutrient management for maximizing sericultural efficiency.

3. Artificial Diets for Silkworm Rearing

3.1 Formulation and components

Efforts to formulate artificial diets for *Bombyx mori* arise from a practical need to decouple silkworm rearing from the spatial, seasonal and labor constraints inherent to mulberry cultivation, while retaining the physiological benefits of a leaf-based diet. Most formulations therefore retain mulberry leaf powder as a non-negotiable core component, reflecting its unique biochemical cues and phagostimulatory properties that remain difficult to replicate synthetically. To this foundation are added alternative protein sources, including soybean meal and blood meal, intended to sustain nitrogen supply and metabolic throughput, though their effectiveness is often instar-specific and sensitive to inclusion rates (Kanta *et al.* 2008, Mottaghitlab and Pourali, 2004, Ekastuti, 2013, Mangammal and Devi, 2012)^[42, 68, 29, 62]. Energy substrates and structural binders such as potato starch, wheat flour and agar serve dual roles by supporting carbohydrate metabolism while conferring the physical stability necessary for uniform ingestion, whereas supplements like sucrose, cellulose and rice bran are incorporated to better approximate the compositional and functional complexity of fresh mulberry foliage (Mottaghitlab and Pourali, 2004, Sahara *et al.* 2001)^[68, 90].

Recognizing the changing nutritional demands across larval development, many artificial systems adopt stage-specific formulations commonly designated as Starter, Grower and Producer diets to align nutrient density and texture with instar-level physiological requirements (Santoso, 2013)^[91]. Yet formulation remains constrained by economics as much as biology, prompting continual trade-offs between ingredient cost and performance outcomes (Mottaghitlab and Pourali, 2004)^[68]. While some diets yield heavier

cocoons under controlled conditions, deficits in shell ratio, filament uniformity, or survival rate often persist relative to conventional mulberry feeding, underscoring unresolved mismatches in nutrient balance and bioavailability (Santoso, 2013, Eleawa and Waked, 2015) ^[91, 30]. These limitations suggest that artificial diets are not merely substitutes but experimental platforms, whose future success depends on greater nutritional precision, improved ingredient synergy and a deeper understanding of silkworm digestive and sensory physiology.

3.2 Advantages and limitations

Artificial diets offer clear strategic advantages where reliance on fresh mulberry foliage constrains rearing intensity or continuity. By reducing exposure to field-borne pathogens, shortening larval duration, and enabling year-round production independent of leaf availability, these diets can stabilize output in regions marked by seasonal or spatial limitations in mulberry supply (Avramova and Grekov, 2013, Mottaghitlab and Pourali, 2004) ^[5, 68]. When carefully formulated, they support robust larval growth and increases in cocoon weight, and their compositional flexibility allows targeted manipulation of nutrient ratios to improve feed conversion efficiency and silk productivity. In practice, the most consistent gains are often observed when artificial diets are deployed as supplements rather than wholesale replacements, complementing mulberry feeding during critical growth phases (Ekastuti, 2013) ^[29].

At the same time, the limitations of artificial diets reveal how closely silkworm performance is tied to the biochemical and physical complexity of natural leaves. No single formulation has yet proven adequate across all larval stages, and many diets fail to replicate the full nutritional spectrum of mulberry, leading to suboptimal biomass conversion and variable cocoon traits (De Bortoli *et al.* 2015, Saviane *et al.* 2014) ^[25, 93]. High-protein diets, particularly those relying heavily on soybean meal, can inadvertently elevate oxygen demand and depress digestibility in later instars, with adverse effects on development and silk characteristics (Rajaram *et al.* 2012) ^[84]. These constraints underscore the need for precise nutrient calibration, stage-specific formulation, and sensitivity to strain-level physiological differences, as silkworm breeds vary markedly in their adaptability to artificial feeding (Guncheva, 2016, Santoso, 2013) ^[33, 91]. Viewed in this light, artificial diets are best understood not as universal substitutes but as context-dependent tools whose value lies in strategic integration with mulberry-based systems and continued refinement through physiological and nutritional research.

3.3 Comparative performance with mulberry-fed silkworms

Comparative evaluations consistently reaffirm the biological advantage of mulberry-based feeding, reflecting the deep evolutionary alignment between *Bombyx mori* physiology and the biochemical complexity of its natural host plant. Larvae reared on fresh mulberry leaves typically exhibit faster growth, more synchronized development and superior cocoon and filament traits, outcomes attributed to the balanced provision of amino acids, readily metabolizable carbohydrates, structural lipids and secondary metabolites that collectively support silk protein biosynthesis and metabolic homeostasis. In contrast, artificial diets, despite

nutritional adequacy on paper, often elicit signs of metabolic strain, including elevated urea and citric acid levels and disruptions across amino acid, lipid and carbohydrate metabolic pathways, indicative of incomplete nutrient assimilation or altered regulatory control (Qin *et al.* 2020, Dong *et al.* 2018) ^[79, 27]. These physiological perturbations frequently manifest as prolonged larval and pupal durations and less predictable developmental trajectories, although carefully designed formulations can partially offset such effects, particularly when artificial diets are restricted to early instars and followed by mulberry feeding during later, silk-intensive stages (Mottaghitlab and Pourali, 2004, Tungjitwitayakul and Tatum, 2017, Dong *et al.* 2017) ^[68, 105, 28].

Beyond growth metrics, artificial rearing systems also reshape internal biological networks. Reduced gut microbial diversity and altered digestive enzyme profiles have been repeatedly observed, with downstream consequences for nutrient metabolism, immune competence, and detoxification capacity an outcome consistent with the silkworm's long-standing specialization for mulberry-derived substrates (Cui, 2005, Rajaram *et al.* 2012) ^[23, 84]. These shifts increase sensitivity to xenobiotics and may compromise resilience under intensive rearing conditions. Nonetheless, the logistical advantages of artificial diets particularly their consistency and independence from seasonal leaf supply remain compelling in resource-limited contexts. Mixed feeding strategies, which leverage artificial diets for early-stage stability and mulberry leaves for late-stage physiological optimization, have emerged as pragmatic compromises that preserve acceptable biological performance while enhancing operational flexibility (Mahmoud, 2013, Bian *et al.* 2022) ^[59, 10]. Taken together, these comparisons underscore that while artificial diets can support survival and basic development, matching the nutritional and functional richness of mulberry leaves remains a central challenge, one that continues to define the trajectory of diet innovation in modern sericulture.

4. Effect of Nutrition on Cocoon Yield and Silk Quality

The conversion efficiency of ingested nutrients into silk by *Bombyx mori* fundamentally determines cocoon yield and fiber quality, placing nutrition at the core of sericultural productivity rather than as a secondary management factor. The biochemical composition of mulberry leaves particularly the balance of proteins, carbohydrates and minerals directly regulates larval growth, silk gland enlargement, and the rate of fibroin and sericin synthesis. Regular feeding schedules, generally three to four feedings per day, help maintain stable metabolic activity and are consistently linked with higher survival, increased cocoon weight and longer, more uniform filaments (Raghuvanshi *et al.* 2019) ^[80].

Beyond basic feeding practices, strategic dietary supplementation has proven effective in enhancing cocoon and silk traits. Additives such as honey, glucose, vitamins and milk improve metabolic efficiency and lead to marked gains in cocoon weight, shell percentage and filament uniformity (Sudha *et al.* 2023, Bhatti *et al.* 2019) ^[97, 9]. Micronutrients further refine these responses; zinc improves shell ratio and raw silk recovery, while imbalances in calcium, magnesium and sulfur negatively affect larval development and cocoon formation (Yungen, 2000, Hossain *et al.* 2015) ^[109, 37]. Improvements in mulberry nutrition

through organic fertilization and plant-based enhancers also elevate leaf quality, larval biomass, silk gland weight, and cocoon yield, highlighting nutrition as an integrated continuum linking plant health, feeding strategy and larval physiology (Rath *et al.* 2004, Sujathamma *et al.* 2014)^[86, 98].

4.1 Cocoon Weight, Shell Ratio and Filament Length

Cocoon weight, shell ratio and filament length are among the most nutrition-sensitive traits influencing commercial silk value, reflecting cumulative dietary effects on larval growth and silk gland productivity. Cocoon weight responds strongly to dietary enrichment with biologically active supplements such as royal jelly, probiotics (*e.g.*, normagut at 2%), Spirulina (300 ppm) and mineral salts including zinc, magnesium and potassium, producing heavier cocoons in the range of 2.13-2.30 g through improved nutrient assimilation during late instars (Nguku *et al.* 2007, Raghuvanshi *et al.* 2019, Anisha *et al.* 2022, Kumar *et al.* 2009, Muruges, 2020)^[75, 80, 3, 53, 72].

Increases in shell ratio indicate that enhanced cocoon weight reflects more efficient allocation of nutrients to silk protein synthesis rather than generalized biomass gain. Dietary inputs such as *Zea mays* flour, probiotics, and mineral supplementation have raised shell ratios beyond 24%, demonstrating improved fibroin deposition (Dahi *et al.* 2016, Raghuvanshi *et al.* 2019, Muruges, 2020)^[24, 80, 72]. Filament length shows similar responsiveness, with higher feeding frequency and supplements like Spirulina and mineral fortification extending filament length, in some cases beyond 1,400 m (Rathod *et al.* 2015, Anisha *et al.* 2022, Kumar *et al.* 2009)^[48, 3, 53]. While these findings highlight the nutritional plasticity of silk traits, their large-scale application requires balancing productivity gains with economic feasibility and environmental sustainability.

4.2 Silk Protein Composition (Fibroin and Sericin)

Silk quality is ultimately governed by the synthesis and structural organization of fibroin and sericin, processes that are highly responsive to larval nutrition. Dietary interventions that enhance silk gland metabolism lead to measurable increases in silk protein deposition. Feeding mulberry leaves treated with cow milk has been shown to increase larval biomass, cocoon weight and shell weight, indicating enhanced fibroin and sericin biosynthesis and more efficient protein accumulation within the cocoon (Hossain *et al.* 2015)^[37].

More targeted nutritional strategies further emphasize this relationship. Feeding sericin-treated leaves significantly improves cocoon output, suggesting that exogenous sericin functions both as a nutrient source and as a regulator of endogenous silk protein synthesis (Hossain *et al.* 2022)^[36]. Mineral supplementation with zinc, magnesium, and potassium supports enzymatic activity and secretory processes in silk glands, resulting in increased fibroin and sericin content and improved silk quality parameters (Kwak *et al.* 2017)^[56]. Nutrition also influences protein structure, higher sericin levels delay fibroin β -sheet formation, promoting a more stable Silk I conformation that enhances fiber integrity (Chithrashree *et al.* 2021)^[22]. However, excessive or imbalanced supplementation, especially under suboptimal environmental conditions, can disrupt protein synthesis and folding, underscoring the need for carefully calibrated nutritional management (Muruges, 2020)^[72].

4.3 Influence of Nutrition on Raw Silk Quality

Raw silk quality reflects the integrated effects of larval diet, silk gland function, and precision of fiber formation, making it highly sensitive to nutritional inputs. Fortification of mulberry leaves with readily assimilable supplements such as honey, glucose, B-complex vitamins, lemon extract and calciferol improves larval metabolism and cocoon development, resulting in better filament continuity and higher raw silk recovery (Sudha *et al.* 2023)^[97]. Protein-rich additives exert particularly strong effects; egg albumen supplementation at moderate levels (20%) significantly increases filament length and raw silk percentage by enhancing amino acid availability during peak silk synthesis (Islam *et al.* 2020)^[38].

Comparable improvements are observed when larvae are fed mineral-rich mulberry varieties such as Jorhat and TR10, where elevated calcium, potassium, magnesium and phosphorus support fibroin accumulation and increase filament output (Ruth *et al.* 2019)^[89]. Milk-treated mulberry leaves further demonstrate nutritional synergy, with milk-fed larvae showing rapid biomass gain during the fifth instar and substantial increases in cocoon weight, shell percentage and reelable silk length (Naik and Somashekar, 2006, Hossain *et al.* 2015)^[73, 37]. These benefits, however, remain highly dependent on environmental stability; deviations in temperature or mineral balance can quickly impair silk gland activity and raw silk quality, emphasizing the need for synchronized nutritional and rearing management (Bekkamov and Samatova, 2023)^[6].

5. Impact of Nutrition on Silkworm Growth and Physiology

5.1 Growth Rate and Larval Health

Larval growth rate and physiological fitness in *Bombyx mori* are strongly regulated by nutrition, which governs developmental tempo and determines subsequent silk production potential. Diets enriched with easily assimilable energy sources and bioactive compounds accelerate growth while supporting silk gland maturation. Supplementation of mulberry leaves with honey, glucose, B-complex vitamins, citrus extracts, or calciferol enhances larval biomass accumulation and cocoon traits by stabilizing metabolic processes during the nutritionally intensive late instars (Sudha *et al.* 2023)^[97]. Antioxidant supplementation, particularly vitamin C administered during the fourth and fifth instars, further promotes silk gland development, resulting in increased larval length, body weight and cocoon quality (Borah and Boro, 2020)^[15].

Comparable growth-enhancing effects have been observed with honey-based diets, which improve protein synthesis in silk glands and increase raw silk recovery (Subhan *et al.* 2013)^[96]. Leaf quality itself plays a decisive role; nutritionally superior mulberry varieties such as *Morus nigra*, characterized by higher protein and carbohydrate content, consistently support heavier larvae and improved cocoon traits (Muhammed and Ayoub, 2023)^[70]. Biological inputs such as probiotics (*Saccharomyces cerevisiae*) enhance digestive efficiency and somatic growth, while increased feeding frequency ensures continuous nutrient and water supply, improving survivability and reproductive fitness (Saritha and Prasad, 2022, Yadav and Bagdi, 2016)^[92, 107]. Together, these findings highlight that larval health depends on nutrient balance, timing, and bioavailability.

rather than nutrient quantity alone, emphasizing the need for growth-optimized yet sustainable feeding strategies.

5.2 Immunity and Disease Resistance

Immune competence in *Bombyx mori* is closely linked to nutritional status, with diet quality shaping both basal resilience and resistance to pathogens. Nutrient-rich mulberry leaves promote stronger immune responses and lower disease incidence, whereas nutritionally poor or excessively tender foliage increases vulnerability to pathogens such as *Beauveria bassiana*, as indicated by reduced LT₅₀ values (Borah and Boro, 2020) [15]. Similar trends are reported under artificial rearing systems, where the inclusion of mulberry leaf powder in formulated diets improves resistance to viral infections, underscoring the immunomodulatory role of host-plant nutrients.

Functional dietary supplements further enhance immune performance. Probiotic supplementation with *Saccharomyces cerevisiae* and *Bifidobacterium bifidum* increases digestive enzyme activity, particularly amylase and invertase, improving nutrient assimilation, larval growth and cocoon traits while indirectly strengthening immune defenses (Chandrasekharan and Nataraju, 2013, Esaivani *et al.* 2014) [21, 31]. Micronutrient enrichment and bioactive supplements also improve disease tolerance and survival under stress conditions (Chandrakala *et al.* 2007) [20]. However, nutritional effects interact with genetic background, pathogen virulence, and rearing environment, indicating that effective disease management requires integrated nutritional, environmental and genetic strategies rather than nutrition alone.

5.3 Energy Metabolism

Energy metabolism forms the physiological link between nutrient intake and silk productivity in *Bombyx mori*, translating diet quality into growth efficiency and silk biosynthesis. Nutritional modulation alters enzyme activity and substrate flow across developmental stages. Honey-enriched mulberry diets enhance glycolysis and oxidative phosphorylation, with aspartate aminotransferase playing a key role during larval and pupal stages, while glutamate dehydrogenase activity predominates in adults (Prasad and Madhavi, 2020) [78]. These diets promote efficient energy utilization without imposing metabolic stress, unlike many artificial feeding regimes.

Silkworms reared on artificial diets often exhibit disrupted amino acid metabolism, reduced carbohydrate and lipid turnover and accumulation of nitrogenous wastes such as urea and uric acid, reflecting incomplete vitamin supply and metabolic imbalance rather than absolute nutrient deficiency (Dong *et al.* 2017) [27]. Biological variation further influences energy dynamics; Tasar silkworms show higher metabolic rates and silk yield than mulberry silkworms, while extended feeding duration improves nutrient conversion efficiency across strains (Kumari *et al.* 2011, Koilpillai, 1995) [55, 49]. Emerging interventions, including TiO₂ nanoparticles and mineral-enriched diets, enhance insulin signaling and bioenergetic efficiency, reinforcing that metabolic harmony rather than nutrient excess is essential for sustaining energy efficiency and silk productivity (Tian *et al.* 2016; Borah and Boro, 2020) [104, 15].

6. Conclusion

This review emphasizes that silkworm nutrition must be viewed as an integrated biological system rather than a set of isolated dietary inputs, wherein mulberry leaf biochemistry, larval physiology, metabolic regulation and the rearing environment interact to shape silk productivity. Across the literature, improvements in cocoon yield and silk quality consistently arise not from nutrient abundance alone but from nutritional balance, appropriate timing and bioavailability. Proteins, carbohydrates, lipids, micronutrients and water function through interconnected metabolic pathways that regulate growth dynamics, immune competence, energy allocation and the synthesis and structural organization of fibroin and sericin. When these interactions are optimally aligned as in high-quality mulberry-based feeding supplemented in a targeted manner, silkworms exhibit marked physiological plasticity and enhanced performance. In contrast, nutritional imbalances, whether due to excessive fortification or poorly calibrated artificial diets, frequently result in metabolic stress, developmental instability and compromised silk quality.

The reviewed studies also reveal a persistent gap between experimental promise and field-level applicability. Although many nutritional interventions yield significant gains under controlled conditions, their translation into commercial sericulture is often constrained by economic feasibility, labor requirements and environmental sensitivity. Artificial diets, despite clear logistical advantages, continue to fall short of reproducing the biochemical complexity and functional efficacy of mulberry leaves, highlighting critical gaps in knowledge related to silkworm digestive physiology, gut-microbiome interactions, and nutrient signaling mechanisms. Moreover, heterogeneity in experimental designs, silkworm strains and rearing environments limits cross-study comparability and the generalizability of findings. Future advances will depend on integrative, systems-level frameworks that bridge molecular biology, plant science, insect physiology and agroecology, alongside rigorous validation of emerging strategies such as precision nutrient delivery, microbiome-informed feeding, nano-enabled supplementation and climate-resilient mulberry management under realistic production settings. Ultimately, sustainable and resilient improvements in silk productivity will require moving beyond additive nutritional interventions toward biologically coherent and ecologically grounded nutritional system design.

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