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Biofortification of mulberry leaves for enhanced silkworm nutrition, immunity, and silk productivity: A review

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Abstract
Mulberry (Morus spp.) is the sole food plant of the domesticated silkworm, *Bombyx mori* L.. Silk productivity is primarily determined by the nutritional quality of mulberry leaves. Continuous use of fertilizers for decades have sustained leaf yield but has rarely targeted the biochemical composition that silkworm physiology requires. Biofortification is the process of enrichment of protein, micronutrient, and antioxidant concentrations in the harvested leaf, which offers a route to close this gap without additional land or labour. This review synthesizes published evidence across four biofortification strategies for mulberry (i) agronomic mineral management, (ii) microbial and biostimulant inoculation, (iii) nanotechnology enabled nutrient delivery and (iv) genetic variation in leaf composition. For each strategy, mechanisms of nutrient uptake and leaf accumulation are examined alongside documented effects on silkworm nutritional indices, immune competence, and cocoon and silk quality traits. This review also evaluates the comparative advantages and limitations of the four strategies, their practical relevance for smallholder sericulture, and the research priorities, standardized multi-site trials, mechanistic and multi-omic studies, and food-chain safety validation foremost among them, that would move the field from proof-of-concept toward farm-scale recommendation.

Keywords: Biofortification, leaf quality, silkworm, nutrients, genetic improvement, nanotechnology

Introduction

1. Sericulture, Mulberry Nutrition, and the Need for Biofortification

Sericulture converts a plant-based input directly into a high-value natural textile fiber and supports more than 60 million people worldwide across production, reeling, weaving, and trade, with China and India together accounting for the majority of raw silk output [1]. *Bombyx mori* is strictly monophagous: every gram of fibroin and sericin deposited in the cocoon, and every antioxidant enzyme mounted against disease, originates from amino acids and minerals absorbed through the midgut from mulberry leaf. The leaf is the entire biochemical substrate for silk production and larval survival, yet its composition varies enormously. Crude protein in *Morus alba* ranges from approximately 15% to 28% dry weight depending on variety, soil nitrogen status, irrigation, pruning cycle, and season, and micronutrient concentrations, particularly zinc, iron, and selenium, are rarely optimized under standard farming practice [2, 3].

Climate change compounds this variability. Elevated CO2 increases leaf carbohydrate content but dilutes protein and mineral concentrations, a pattern established across crop species and increasingly documented in mulberry, while heat stress reduces leaf moisture and soluble protein and drought cycles shorten the effective feeding period between irrigations [4, 5]. Conventional fertilization, optimized for yield rather than composition, does little to correct these deficits.

2. Biofortification: Concept, Strategies, and Review Objectives

Bouis and Welch [6] defined biofortification as the process of increasing the nutritional quality of food crops through agronomic practice, conventional breeding, or biotechnology, and White and Broadley [5] identified soil application, foliar application, and genetic improvement as the three principal pathways. Applied to mulberry, biofortification differs from conventional crop biofortification in one important respect: the target consumer is a lepidopteran larva rather than the human digestive system, so leaf-level concentration and biochemical accessibility to the silkworm gut, rather than human bioavailability, define success.

Four strategy categories are now recognized. Agronomic biofortification applies soil or foliar mineral inputs, most effectively for zinc, selenium, and silicon, which are prone to soil immobilization and respond well to direct leaf delivery [7]. Microbial biofortification exploits rhizosphere organisms, including nitrogen-fixing and phosphate-solubilizing bacteria and mycorrhizal fungi, to mobilize nutrients already present but chemically unavailable in soil [8, 9]. Nano-enabled biofortification uses particles in the 1 to 100 nm range that penetrate stomata and cuticle pores and dissolve gradually, extending nutrient availability beyond a single spray [10, 11]. Genetic biofortification exploits existing varietal differences in root uptake efficiency and leaf-level nutrient retention, offering a pathway independent of external inputs. An early parallel to agronomic biofortification is the demonstration that Azotobacter foliar

application can match full chemical nitrogen dosing for mulberry leaf yield [12].

This review synthesizes published evidence across these four strategies. For each, we examine mechanisms of leaf accumulation, effects on silkworm nutrition and immune function, and implications for cocoon and silk quality, and we close by identifying the research gaps and priorities that would move the field from proof-of-concept to farm-scale practice.

Nutritional Composition of Mulberry Leaves and Silkworm Performance

Mulberry leaf nutritional value for silkworms' rests primarily on its protein fraction, which typically ranges from 15% to 28% dry weight; younger apical leaves carry more protein and moisture but also higher phenolic concentrations that can depress digestibility [2]. *Bombyx mori* cannot synthesize ten essential amino acids and depends entirely on leaf tissue for leucine, isoleucine, valine, threonine, lysine, methionine, phenylalanine, tryptophan, histidine, and arginine. Glycine and alanine together make up approximately 60% of silk fibroin, while serine and tyrosine are more sensitive to leaf nutritional status and serve as diagnostic markers of leaf quality in silk protein research.

Soluble sugars, ranging from 8% to 20% dry weight, govern larval food intake rate and digestive efficiency and respond strongly to nitrogen fertilization, irrigation, and pruning interval. Crude fiber (12% to 18%) is nutritionally inert and dilutes the energy-available fraction of the leaf. Among minerals, zinc functions as a cofactor for more than 300 enzyme systems and is critical for protein synthesis and antioxidant defense; soil zinc deficiency is common across the red laterite soils of Karnataka, Andhra Pradesh, and West Bengal, translating directly into suboptimal leaf zinc [13, 4]. Selenium, required only in trace amounts, is a structural component of glutathione peroxidase and directly supports oxidative stress management in the larva.

Mulberry leaves also contain chlorogenic acid, caffeic acid, rutin, quercetin, and kaempferol glycosides. At moderate concentrations these phenolics scavenge reactive oxygen species in the midgut and hemolymph; at high concentrations, particularly in very young leaves, they form polyphenol-protein complexes that reduce digestibility through tannin-like mechanisms. The iminosugar 1-deoxynojirimycin, present at 0.1% to 0.3% dry weight, inhibits insect trehalase activity but does not impair performance at typical leaf concentrations. Biofortification strategies that alter secondary metabolite profiles must account for this dual character.

Leaf composition responds jointly to variety, soil fertility, nitrogen management, irrigation, pruning cycle, season, and leaf position on the branch. A study of Central European local mulberry genotypes found that protein content, individual phenolics, and microelement concentrations differed significantly between varieties and predicted silkworm performance parameters directly, confirming that variety selection and agronomic management jointly determine the nutritional quality silkworms receive [14].

Table 1: Representative nutritional composition of Morus alba leaves (dry weight basis). Sources: [3, 2, 14, 15].

Parameter	Typical Range	Optimal for Silkworm	Notes
Crude protein	15-28% DW	> 20%	Declines with leaf age
Soluble sugars	8-20% DW	> 14%	Variety and season dependent
Crude fiber	12-18% DW	< 15%	Inversely related to digestibility
Crude fat	3-6% DW	4-5%	Fatty acid profile affects silk gland lipids
Moisture (fresh leaf)	70-82%	> 75%	Higher in young leaves
Calcium	1.2-2.5% DW	1.8-2.2%	Cuticle hardening, silk gland activity
Zinc	15-45 mg/kg	30-40 mg/kg	Often limiting in Indian soils
Iron	80-200 mg/kg	100-150 mg/kg	Varies with soil pH
Selenium	0.01-0.15 mg/kg	0.05-0.10 mg/kg	Geographically variable
Total phenolics	2-8% DW	3-5%	High levels depress digestibility
Chlorophyll	0.8-2.5 mg/g FW	> 1.8 mg/g	Positively related to protein

Agronomic Biofortification

Nitrogen is the primary driver of mulberry leaf protein and yield. Irrigated Indian plantations typically receive 300 kg N/ha per year in split doses after each pruning; timing applications to coincide with rapid leaf expansion, approximately 25 to 35 days after pruning, maximizes protein accumulation without the leaching risk associated with excess nitrogen.

Zinc biofortification relies on foliar application (0.5% ZnSO4 or an equivalent chelated form), which bypasses soil immobilization and is more reliable than soil application on laterite soils above pH 6.5 [7]. Zinc functions in mulberry as a cofactor for RNA polymerase, carbonic anhydrase, and alcohol dehydrogenase, and its foliar delivery simultaneously supports Cu/Zn-superoxide dismutase activity in silkworm hemocytes, linking a single agronomic input to both leaf-level photosynthetic efficiency and larval immune competence [13, 4].

Selenium biofortification is more delicate because the margin between beneficial and toxic concentrations is narrow. Foliar selenate at 10 to 50 g Se/ha raises leaf selenium from near-zero to nutritionally meaningful levels without phytotoxicity. Direct dietary selenium supplementation in silkworms improved larval weight, cocoon weight, pupal weight, and fecundity at 50 micromolar, with growth inhibition above 150 micromolar [16]. Notably, a dietary trial using an organic selenium compound delivered through natural mulberry leaf found no significant effect on cocoon performance, suggesting that leaf-level selenium delivery at field-relevant concentrations may differ in bioavailability from direct dietary supplementation [17]; this discrepancy is an important design consideration for field biofortification programs and is revisited in the research gaps section.

Silicon, deposited in leaf epidermal cell walls, increases leaf rigidity, reduces transpirational water loss, and lowers fungal disease and mite feeding damage, with particular

value in semi-arid sericulture zones [18]; any reduction in palatability from increased epidermal hardness appears outweighed by these stress-tolerance benefits at practical application rates. Boron, calcium, and magnesium play more localized roles in phloem sugar transport, cell wall integrity, and chlorophyll synthesis respectively.

Nano-Enabled Biofortification

Conventional mulberry fertilization faces two practical constraints: soil-applied zinc and iron are rapidly immobilized through adsorption and precipitation, and foliar-applied conventional fertilizers cause stomatal and cuticle damage at concentrations high enough to be agronomically useful. Nanoparticles in the 1 to 100 nm range address both problems. Their size allows penetration through stomata and cuticle pores below the phytotoxicity threshold, and their gradual dissolution sustains nutrient release over days to weeks rather than a single spray event [10, 11]. This behavior likely operates through three complementary pathways: ionic supply that matches metabolic demand rather than flooding transporters, direct stomatal penetration that may stimulate defense-related metabolite production, and sustained availability that reduces the mid-cycle nutritional stress typical of fixed-schedule fertilization.

Field trials at the UAS, Dharwad, evaluated foliar nano NPK (19:19:19) on mulberry variety V1 across two seasons. At 6 g/L, nano NPK produced the highest recorded values for SPAD chlorophyll index (39.98), soluble protein (13.76%), total sugars (15.86%), and leaf yield (747.94 g/plant), exceeding both conventional NPK and lower nanofertilizer doses, with corresponding improvements in larval growth and cocoon and silk traits in companion feeding trials [19].

Zinc oxide nanoparticles (20 to 100 nm) consistently improve photosynthetic efficiency, protein content, and antioxidant enzyme activity across crop species; in rice, foliar and soil-applied ZnO nanoparticles increased zinc content in above-ground tissue relative to bulk ZnSO4 at equivalent applied rates [20]. Mulberry-specific ZnO nanoparticle data remain limited, though the underlying mechanism, gradual dissolution in the apoplast releasing Zn2+ that activates carbonic anhydrase and chloroplastic Cu/Zn-SOD, is directly applicable; at high doses (above 500 mg/L foliar), ZnO nanoparticles generate reactive oxygen species themselves, making dose optimization essential before field recommendation. Silicon and iron oxide nanoparticles show comparable promise, penetrating tissue more readily than bulk forms and mimicking siderophore-mediated iron release in the rhizosphere, though mulberry-specific trials remain sparse. Nano-selenium, taken up through endocytosis-like mechanisms rather than selenate transporters, appears less prone to phytotoxicity at equivalent selenium doses and represents an unexplored but mechanistically attractive tool given the narrow therapeutic window of selenium.

The environmental fate of metal-based nanoparticles applied to mulberry has not been systematically addressed. ZnO and TiO2 nanoparticles persist in soil and may accumulate in root zones with repeated application, and their effects on nitrogen-fixing bacteria and mycorrhizal fungi supporting organic mulberry farming are not well characterized. Nanoparticle transfer from leaf to silkworm tissue is essentially unstudied for this system, and field-scale recommendations should wait for this baseline safety data.

Table 2: Agronomic and nano-enabled biofortification interventions in mulberry: published evidence.

Intervention	Method Dose	Key Response	Source
Nitrogen via Azotobacter + 50% chemical N	Foliar biofertilizer	Leaf yield exceeded full chemical N treatment	Sudhakar et al. (2000)
Zinc (ZnSO4)	Foliar spray, 0.5%	Increased leaf protein and chlorophyll; reduced oxidative damage	Cakmak (2008)
Selenium (selenate)	Foliar / diet, 50 µM optimal	Increased larval, cocoon, and pupal weight	Zhu et al. (2019)
Silicon	Soil or foliar silicate	Improved stress tolerance; reduced fungal disease	Epstein (1999)
Nano NPK (19:19:19)	Foliar, 6 g/L	Highest SPAD, protein, sugar, and yield; best cocoon traits	Banuprakash & Narayana Reddy (2024)
ZnO nanoparticles	Foliar / soil, 20-100 nm	Increased tissue zinc vs. bulk ZnSO4 (rice)	Mi et al. (2023)
TiO2 nanoparticles	Dietary (direct)	14.88-fold increase in BmNPV resistance	Ye et al. (2015)
Organic selenium compound (nano-relevant delivery)	Dietary via leaf	Enhanced thermotolerance; modified hemolymph amino acid profile	Zhang et al. (2026)

Microbial and Biostimulant-Based Biofortification

Azotobacter chroococcum is the most extensively studied plant growth-promoting rhizobacterium (PGPR) for mulberry. In a two-year field trial at the Central Sericultural Research and Training Institute, Berhampore, foliar Azotobacter applied with half the recommended nitrogen dose produced leaf yield significantly greater than the full chemical nitrogen treatment [12]. Azospirillum brasilense contributes through a different mechanism, producing nitric oxide and ethylene that stimulate root branching and expand the root surface area available for nutrient absorption [22, 9].

Vesicular arbuscular mycorrhizal (VAM) fungi form obligate symbioses with roughly 80% of terrestrial plant species, including mulberry, extending hyphae 8 to 10 cm beyond the root surface into soil microvolumes where phosphorus and zinc are otherwise inaccessible to roots directly [8]. VAM inoculation under semi-arid conditions has been reported in extension and field literature to improve leaf quality and cocoon traits relative to uninoculated controls, though rigorously controlled, VAM trials with cocoon-level outcomes in mulberry remain uncommon, and results should be extrapolated with caution pending further validation.

Endophytic bacteria colonizing internal mulberry tissue without disease symptoms contribute indirectly to nutritional biofortification through disease suppression.

Burkholderia cepacia strain Lu10-1, isolated from mulberry leaves, colonizes seedling tissue rapidly, produces auxins, contributes to phosphate solubilization, and is antagonistic to Colletotrichum dematium, the causal agent of mulberry anthracnose, suppressing disease development when applied to leaves or soil [23]. By preventing the protein and pigment losses that disease lesions cause, such endophytes protect leaf nutritional integrity even without a direct nutrient-fortification mechanism of their own. A related line of evidence on biocontrol residues is informative here: Trichoderma harzianum applied against mulberry powdery mildew, when treated leaves were fed to silkworms after the recommended safety interval, was associated with the highest recorded cocoon weight, shell weight, and shell ratio among the biocontrol agents tested, indicating that microbial inputs selected for plant protection can carry a nutritional dividend for the silkworm alongside their disease-management benefit [24].

Seaweed-derived biostimulants based on Ascophyllum nodosum and Ecklonia maxima, applied as foliar sprays at 2 to 5 mL/L, contain betaines, polyamines, cytokinins, and oligosaccharides; Indian sericulture extension literature reports increased leaf yield and chlorophyll content, though peer-reviewed mechanistic studies specific to mulberry remain limited. Humic substances improve soil cation exchange capacity and chelate micronutrients into root-accessible forms. Spirulina biomass, rich in protein (60% to 70% dry weight) and minerals including iron and zinc, provides readily soluble amino acids when applied as a foliar spray or soil amendment and has improved larval growth parameters in direct-feeding trials; its use as a mulberry soil or foliar biofortification input is scientifically plausible but has not been directly validated.

Effects of Biofortified Leaf on Silkworm Physiology

Silkworm nutritional performance is quantified through standardized indices: approximate digestibility (the fraction of ingested food absorbed), efficiency of conversion of digested food, and efficiency of conversion of ingested food, which integrates both. Biofortified mulberry leaf consistently raises these indices relative to conventionally managed leaf. Higher protein concentration increases conversion efficiency by supplying more amino acids per unit leaf consumed; higher soluble sugar increases digestibility by providing energy for active nutrient transport across the midgut epithelium; and lower fiber content reduces the non-digestible fraction, improving both measures simultaneously.

Larval weight at spinning reflects protein assimilation efficiency across the five larval instars, during which body weight increases roughly 10,000-fold. The fifth instar alone accounts for approximately 80% of total silk gland growth and fibroin synthesis, making leaf nutritional quality during this stage disproportionately important for cocoon outcomes. In trials comparing nano NPK-treated mulberry against conventionally fertilized plants, fifth-instar larvae showed significantly higher daily weight gain, reached peak weight one to two days earlier, and produced more uniform cocoon weights over a shorter spinning period.

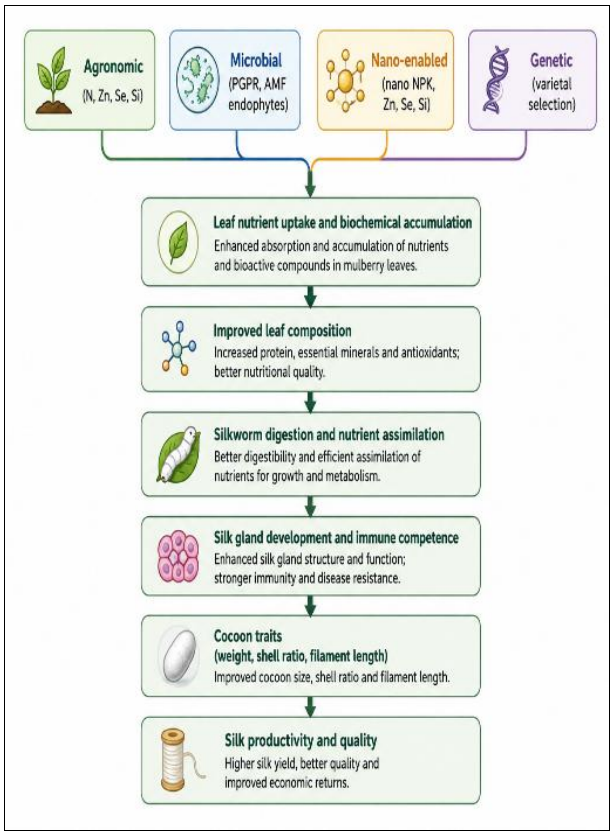

Fig 1: Integrated mechanism flowchart linking biofortification strategy inputs to silk productivity outcomes.

Silk gland growth depends directly on systemic amino acid supply from the hemolymph, with the posterior silk gland increasing from approximately 0.1 g to over 2 g during the fifth instar as it fills with fibroin. Zinc supports this process through its role in RNA polymerase and ribosomal protein function, sustaining the high rate of fibroin mRNA translation. A multi-tissue metabolomic study confirmed that mulberry-fed silkworms carry higher concentrations of

key amino acids and energy metabolites in posterior silk gland tissue than formula-fed controls, corresponding to better cocoon performance [25]. Protein- and sugar-rich biofortified leaf also elevates overall digestive enzyme activity relative to nutritionally deficient leaf, which partially explains the improved conversion efficiency observed in feeding trials.

Biofortification and Silkworm Immunity

Bombyx mori relies entirely on innate immunity, expressed through hemolymph antimicrobial peptides and enzymatic cascades and through hemocyte-mediated cellular defense. The prophenoloxidase system is the central enzymatic arm of humoral immunity, and its activity is a direct functional measure of immune competence [26]. Protein-adequate diet maintains hemocyte counts and hemolymph protein levels required for effective immune responses; protein-deficient silkworms show reduced phenoloxidase activity, lower lysozyme levels, and greater susceptibility to bacterial challenge. Zinc, selenium, and mulberry-derived polyphenols support antioxidant enzyme activity in hemocytes, allowing immune cells to manage the oxidative burst of pathogen killing without self-damage; zinc deficiency specifically reduces antimicrobial peptide production across several insect systems.

Bacterial flacherie, viral nuclear and cytoplasmic polyhedrosis diseases, muscardine, and pebrine remain the dominant disease threats in sericulture, with BmNPV alone causing losses of approximately 16% of potential silk production in affected rearing cycles. Nutritional status interacts directly with disease resistance: low-dose dietary titanium dioxide nanoparticles increased BmNPV resistance 14.88-fold, reducing mortality from 8.33% to 0.56% at 144 hours post-infection, through inhibition of viral proliferation in the midgut and upregulation of the Bmlipase-1 resistance gene alongside modulation of JAK/STAT and PI3K-Akt signaling [21].

Among the antioxidant enzymes, superoxide dismutase, catalase, glutathione peroxidase, and glutathione reductase all respond to dietary micronutrient supply, with cytoplasmic Cu/Zn-SOD and mitochondrial Mn-SOD requiring adequate zinc and manganese, respectively. Selenium is a structural, irreplaceable component of glutathione peroxidase; selenium deficiency reduces its activity specifically while leaving other antioxidant enzymes largely unaffected, making selenium a particularly targeted biofortification objective for oxidative stress protection.

Influence on Cocoon and Silk Quality

Shell ratio, the dry cocoon shell mass (fibroin plus sericin) expressed as a percentage of fresh cocoon weight, is the primary commercial quality metric; bivoltine hybrids above 20% are considered commercially viable, with the best-performing hybrids under optimal nutrition reaching 23% to 25%. Shell ratio responds reliably to leaf protein quality, since higher dietary protein supports greater fibroin deposition per unit larval biomass independent of total cocoon size. Silkworms fed leaves from mulberry genotypes with higher protein and specific phenolic profiles produced significantly higher shell and cocoon weight than reference varieties, though total phenolic concentration above a threshold correlated negatively with larval performance [14].

Filament length, ranging from approximately 800 to 1,500 m per cocoon in well-managed bivoltine hybrids, depends on fibroin accumulation rate and the physical properties of the fiber during extrusion. Reelability, the percentage of cocoons from which silk unwinds continuously without breakage, falls when fiber cross-section is uneven or sericin coating is insufficient; magnesium and calcium affect sericin gelation, while zinc influences fibroin secondary structure through its effect on disulfide bond formation in the spinning duct. Fibroin constitutes 70% to 80% of the dry cocoon shell and determines tensile strength, while sericin, the glue protein removed during degumming, holds fibroin fibrils together; protein-rich diets tend to shift this ratio toward fibroin, improving thread strength and luster

Table 3: Cocoon and silk quality outcomes across key biofortification treatments.

Treatment	Cocoon Weight	Shell Ratio (%)	Key Additional Effect
Conventional chemical NPK (reference)	~1.8-2.0 g	19-21	Baseline for comparison
Nano NPK, 6 g/L (foliar)	Improved vs. all treatments	Improved	Highest leaf protein, chlorophyll, sugar; shortened larval duration
Selenium, 50 µM (dietary)	Significantly increased	Increased	Increased pupal weight and fecundity
High-protein local genotype	Significantly increased	Increased	Higher shell weight; excess phenolics reduce performance
Trichoderma harzianum biocontrol residue (foliar)	14.99 g	21.17	Longest filament length (769.05 m) among biocontrol treatments
TiO2 nanoparticles (dietary)	—	—	14.88-fold increase in BmNPV resistance

Challenges and Research Gaps

The most pervasive problem in mulberry biofortification research is the absence of standardized experimental protocols. Studies vary in mulberry variety, plantation age, soil type, irrigation regime, climate zone, silkworm hybrid, larval stage at assessment, and analytical method for leaf composition, making cross-study comparison unreliable and preventing meta-analysis. A coordinated international protocol, analogous to the standardized rearing guidelines issued by national sericulture research institutes, would substantially advance the field.

Most published trials were conducted on a single mulberry variety, typically V1 or S-1635 in India, despite clear evidence that cultivars differ in root architecture, cuticle thickness, stomatal density, and secondary metabolite profile, all of which plausibly modulate biofortification response. Multi-variety trials run simultaneously under identical conditions are absent from the literature, as is long-term, field-scale validation tracking leaf quality and silkworm performance across multiple seasons at commercial rearing scale.

The application of metal-based nanoparticles to mulberry represents a food-chain delivery route that has not been

evaluated for nanoparticle transfer from leaf to silkworm tissue, from silkworm to cocoon, or from cocoon to silk-reeling workers. These concerns are particularly acute in mulberry cultivation because the leaf is consumed immediately after harvest without processing. The broader nano-agricultural literature has raised separate concerns about soil microorganism disruption and groundwater contamination that remain unexamined in mulberry systems specifically.

Nanofertilizers, mycorrhizal inoculants, and certified biofertilizer cultures all carry higher per-unit cost than conventional fertilizers, a material constraint given that most mulberry farmers in India and Bangladesh cultivate less than one hectare; published economic analyses of biofortification adoption in mulberry are uncommon. The mechanistic connection between specific leaf metabolites and specific silkworm gene-regulatory events is also largely absent from the literature. Without this mechanistic grounding, biofortification remains empirical and subject to unexplained failures when field conditions deviate from the original experimental setting.

Conclusion

Mulberry leaf biofortification shows clear potential for improving silkworm performance and cocoon quality. Agronomic mineral applications, microbial inoculants, and nanofertilizers have improved leaf nutritional quality and traits such as cocoon weight, pupal weight, fecundity, and leaf yield. However, the available evidence is still limited by the small number of multi-site and long-term studies. Further research should focus on standardized multi-location trials and interdisciplinary studies linking plant nutrition with silkworm physiology, molecular responses, and gut microbiome changes. Understanding nutrient transport and the safety of nanoparticle-based biofortification will also be important for developing effective and sustainable farmer-level practices.

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