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Biological and Industrial Prospects of Polyamines in Silkworms: A Comprehensive Review

Sumalini Bora [a*], Anna Kaushik [a], Priyangana Chetia [a], Toko Naan [b], Bidisha Kashyap [c] and Rubi Sut [a]

[a] Department of Sericulture, FC&RI, Tamil Nadu Agricultural University, Coimbatore, 641003, India.
[b] Division of Sericulture, Sher-e-Kashmir University of Agricultural Science and Technology, Jammu-180009, India.
[c] Department of Sericulture, Assam Agricultural University, Jorhat, 785013, India.

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Polyamines, specifically putrescine, spermidine, and spermine—are low molecular weight aliphatic cations that play essential roles in cellular growth, DNA stabilization, protein synthesis, and stress tolerance across biological systems. In the context of sericulture, recent studies have uncovered the multifaceted impact of polyamines on silkworm physiology, offering new avenues for improving silk yield and quality. This review consolidates current findings on the role of polyamines in regulating the cell cycle, enhancing nutritional indices, improving silk fiber characteristics, and boosting reproductive efficiency in *Bombyx mori*and wild silkworm species such as *Antheraea mylitta*. Supplementation with optimal concentrations of spermidine and spermine has been shown to

**Corresponding author: Email: sumalinibora@gmail.com;*

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promote larval growth, increase silk gland and cocoon weight, upregulate fibroin gene expression, and improve egg production and hatchability. These effects are particularly pronounced in hybrid strains, highlighting the potential of polyamines to exploit hybrid vigour in commercial sericulture. Molecular analyses, including FTIR and SEM, support structural enhancements in silk fibers, while histological studies demonstrate improved reproductive tissue development. Given their low cost, scalability, and ease of integration into existing rearing practices, polyamines present a promising biotechnological tool for sustainable sericulture. The review also identifies future research directions, including polyamine metabolism, dose optimization, and synergistic use with other biostimulants. Overall, polyamines represent a valuable asset for advancing silk production efficiency and quality in both laboratory and field conditions.

Keywords: Polyamines; Bombyx mori; silk production; spermidine; sericulture biotechnology; reproductive physiology.

1. INTRODUCTION

1.1 Overview of Polyamines

Polyamines are low-molecular-weight, polycationic aliphatic amines that are universally present in prokaryotic and eukaryotic cells (Bachrach 2010). The three main types—putrescine, spermidine, and spermine—are synthesized through a pathway initiated by the conversion of ornithine to putrescine via ornithine decarboxylase (ODC), a rate-limiting enzyme (Childs et al., 2003). Spermidine and spermine are subsequently formed by the action of spermidine synthase (SPDS) and spermine synthase (SPMS), with S-adenosyl-methionine decarboxylase (SAMDC) contributing to this conversion (Umekage and Ueda 2006). Polyamines are positively charged at physiological pH, which enables them to interact electrostatically with negatively charged biomolecules such as DNA, RNA, and phospholipids, thereby stabilizing molecular structures and modulating biological functions (Mondal et al. 2007; Thomas et al. 2001).

Due to these interactions, polyamines are implicated in a wide range of cellular processes including DNA replication, gene transcription, translation, cell proliferation, differentiation, membrane stability, and apoptosis (Bardóczet al. 1993; Pardo et al. 1998). In silkworm cells, spermidine has been shown to promote DNA replication and cell cycle progression, whereas inhibitors of polyamine biosynthesis like DFMO (difluoromethylornithine) and MGBG (methylglyoxal bis(guanylhydrazone)) have the opposite effect (Chang et al. 2021). Furthermore, spermidine intake through diet has been linked with enhanced growth, improved antioxidant activity, and even delayed aging in organisms such as *Drosophila melanogaster* and *Caenorhabditis elegans* (Eisenberg et al. 2009; Madeo et al. 2010).

1.2 Significance in Silkworm Biology

The mulberry silkworm, *Bombyx mori* L., is a domesticated lepidopteran insect that plays a central role in global silk production. As a monophagous species feeding exclusively on *Morus indica* leaves, its nutritional and physiological status is directly linked to cocoon and silk yield (Nagaraju 2002; He, et al.2021). Polyamines have emerged as potent regulators in *B. mori* development, particularly during the fifth instar—the most crucial stage for silk synthesis.

Numerous studies have demonstrated that polyamine supplementation can enhance multiple biological and economic parameters in *B. mori*. For example, feeding fifth instar larvae with spermidine (50 µM) and spermine (100 µM) resulted in significant increases in body weight, silk gland mass, cocoon weight, and filament length. Table 1 shows the comparisons of the shell weight of the cocoons treated with and without polyamines (Yerra and Mamillapalli, 2016; Yerra et al. 2017). Moreover, the influence of polyamines treatment on the mechanical properties of silk fiber was evaluated by analyzing fiber diameter, breaking strength, elongation at break, tenacity, moisture regain, and denier in cocoons obtained from control and Spd-treated mulberry-fed larvae (Table 2). It was found that spermidine treatment resulted in an increase in fiber diameter and elongation at break, with a concomitant decrease in denier, breaking strength, and moisture regain, while tenacity remained largely unaffected.

Table 1. Economic parameters of the cocoons treated with polyamines

Treatment	Average filament length	Average shell weight	% Sericin	% Fibrion
Control	824 ± 87.26	0.34 ± 0.005	32.42 ± 1.27	67.57 ± 1.27
Putresine-50	760 ± 20.40	0.35 ± 0.015	32.66 ± 1.75	67.35 ± 1.75
Spermine-50	854 ± 34.16	0.30 ± 0.003	35.4 ± 2.07	64.59 ± 2.07
Spermidine- 50	1024 ± 84.25	0.38 ± 0.005	31.78 ± 1.81	68.21 ± 1.81

Table 2: Mechanical properties of the polyamine treated cocoons

Treatment Regain	Breaking strength in gms	% Elongation at break	% Moisture	Tenacity in gpd	Fiber diameter in microns	Fiber denier
Control	8.76 ± 0.62	12.7 ± 2.15	8.14 ± 0.75	3.63 ± 0.31	15.59 ± 1.32	2.39 ± 0.23
Treated	8.22 ± 0.30	13.1 ± 1.28	7.30 ± 0.39	3.61 ± 0.21	16.45 ± 1.10	2.28 ± 0.20

Although variations were observed between the control and treated groups, the differences were not statistically significant. At the molecular level, spermidine treatment increased fibroin gene (Fib-H) expression in silk glands, contributing to higher silk yield and improved fiber structure (Yerra et al. 2017).

In reproductive biology, polyamines have also shown promising effects. Spermidine and spermine feeding enhanced testicular development and fecundity in both male and female *B. mori* moths, significantly increasing egg production compared to controls (Mysarlaet al. 2016). Similar results were observed in wild silkworms such as *Antheraea mylitta*, where spermidine (50 µM, 100 µM) promoted oogenesis and spermine (50 µM, 100 µM) supported spermatogenesis, as evidenced by increased hatching success in cross-mating experiments (Swamy et al. 2023).

Given the demand for high-quality silk and the importance of improving sericulture productivity, polyamines offer a cost-effective and biologically sound strategy. Their multifunctional roles—in silk protein synthesis, gut microbiota regulation, reproductive enhancement, and cellular protection—highlight their relevance to modern sericultural practices (Rajan et al. 2022; Shahzadi et al. 2022).

2. CELLULAR AND MOLECULAR ROLES OF POLYAMINES

2.1 Regulation of the Cell Cycle

Polyamines are essential polycationic molecules involved in regulating multiple physiological processes, including cell growth, differentiation, and survival. In the context of insect cellular biology, they have drawn increasing attention for their critical role in cell cycle regulation. In *Bombyx mori*, spermidine has been identified as a key polyamine that modulates cell cycle progression in cultured silkworm cells.

A recent study by Chang et al. (2021) utilized BmN cells derived from *B. mori* ovary tissue to evaluate the impact of exogenous spermidine and polyamine synthesis inhibitors on cell proliferation. Their results revealed that treatment with spermidine significantly promoted DNA replication and accelerated progression from the G1 phase to the S phase of the cell cycle. This was attributed to the upregulation of several cell cycle-related genes, including those coding for cyclin proteins and replication enzymes.

Conversely, when cells were treated with difluoromethylornithine (DFMO), a specific inhibitor of ornithine decarboxylase (ODC), and methylglyoxal-bis(guanylhydrazone) (MGBG), an inhibitor of S-adenosylmethionine decarboxylase (SAMDC), a pronounced inhibition of cell cycle progression was observed. The suppression of polyamine biosynthesis led to downregulation of DNA synthesis genes and arrested the cell cycle at the G1/S checkpoint (Chang et al., 2021).

These findings underscore the indispensable role of intracellular polyamine homeostasis in cell proliferation. Similar mechanisms have been documented in mammalian systems, where polyamines are known to stabilize DNA structure, regulate transcription, and assist in ribosome assembly (Childs et al., 2003; Pegg, 2016). The conservation of these functions across taxa highlights the potential of polyamines like spermidine as universal modulators of mitotic activity.

The application of this knowledge in sericulture is significant. Enhanced cell proliferation in silk gland tissues can potentially lead to increased silk protein synthesis, supporting higher cocoon yields and better-quality silk. Understanding the molecular pathways regulated by spermidine also opens avenues for genetic or biochemical manipulation aimed at improving silkworm productivity.

2.2 Enhancement of Nutritional Efficiency and Antioxidant Capacity

In addition to their role in cell division, polyamines—particularly spermidine—contribute to improved metabolic efficiency and physiological resilience in silkworm larvae. The fifth instar is the most critical developmental stage in *Bombyx mori*, during which approximately 85% of total silk proteins are synthesized. Optimizing nutritional uptake and metabolic conversion during this stage is essential for maximizing cocoon production.

Rajan et al. (2022) conducted a comprehensive study to assess how dietary supplementation with spermidine influences nutritional indices and metabolic parameters in *B. mori*. The larvae were fed mulberry leaves fortified with 50 µM spermidine, and multiple indicators of nutritional efficiency were evaluated, including consumption index (CI), approximate digestibility (AD), efficiency of conversion of ingested food (ECI), and efficiency of conversion of digested food (ECD).

The results revealed that spermidine significantly increased all major indices compared to control larvae. This suggests that the compound enhances both ingestion efficiency and metabolic utilization of nutrients. These effects may be linked to the regulatory role of polyamines in protein and carbohydrate metabolism pathways, as well as their stabilizing influence on cellular membranes and enzymes involved in digestion and assimilation.

Beyond nutrient metabolism, the same study also showed that spermidine supplementation elevates intracellular polyamine levels in the larval gut, particularly in the free, conjugated, and bound forms. This elevation coincided with an increase in antioxidant potential, as evidenced by enhanced performance in standard assays such as DPPH radical scavenging, ferric reducing antioxidant power (FRAP), and superoxide dismutase (SOD) activity.

One of the more novel findings was the observation of improved gut microbial diversity and abundance in spermidine-fed larvae. A healthy and diverse gut microbiome is essential for efficient nutrient digestion, vitamin synthesis, and immunity in insects. The modulation of the gut microbial profile by polyamines introduces an indirect mechanism by which larval health and silk productivity may be enhanced (Rajan et al., 2022).

These results collectively demonstrate that polyamines are not only intracellular regulators but also function through microbiome-mediated pathways to optimize growth and development. This dual mechanism of action makes them particularly valuable as dietary supplements in commercial sericulture. By improving both internal metabolic efficiency and external digestive capacity, spermidine offers a holistic approach to boosting silkworm performance under various environmental and nutritional conditions.

3. ENHANCEMENT OF SILK PRODUCTION AND QUALITY

3.1 Improvements in Silk Fiber Properties

Silk production in *Bombyx mori* is a complex physiological process governed by the activity of silk glands, the synthesis of structural proteins such as fibroin and sericin, and the proper spinning of the cocoon filament. Recent advances have highlighted the role of polyamines, particularly spermidine, in augmenting the quantity and quality of silk through both transcriptional and post-transcriptional mechanisms.

In a detailed investigation by Yerra et al. (2017), the dietary supplementation of fifth instar *B. mori* larvae with spermidine (50 µM) led to a significant increase in cocoon filament length, cocoon weight, and shell ratio compared to untreated controls. The study also reported that silk fibers obtained from spermidine-fed larvae were visibly thicker and more robust, as confirmed by measurements of fiber diameter using scanning electron microscopy (SEM). In particular, the average diameter of silk fibers increased from 14.3 µm in controls to 19.2 µm in the treated group (Yerra et al., 2017).

At the molecular level, spermidine treatment was associated with enhanced expression of fibroin heavy chain gene (Fib-H), a key component responsible for the tensile strength and elasticity of silk threads. Quantitative RT-PCR analysis showed a significant upregulation of Fib-H transcripts in silk glands, supporting the hypothesis that spermidine stimulates transcriptional activation of silk structural genes (Yerra et al., 2017). Furthermore, despite the increased silk output, the fibroin-to-sericin protein ratio remained stable, indicating a proportional enhancement in silk gland biosynthetic capacity without compromising the intrinsic composition of the silk fiber.

These findings align with earlier work by Yerra and Mamillapalli (2016), who demonstrated that polyamines influence not just morphological traits like cocoon size but also molecular markers associated with silk gland function and protein biosynthesis. Enhanced fiber elasticity, combined with a stable sericin coating, suggests improved commercial properties such as easier reeling and better fabric texture.

3.2 Molecular Analysis of Silk Components

To further understand the structural and compositional changes induced by polyamine supplementation, advanced physicochemical analyses have been employed. Using FTIR spectroscopy and SEM imaging, Yerra et al. (2017) demonstrated distinct molecular-level alterations in silk fibers derived from spermidine-treated larvae. FTIR spectra revealed slight shifts in the amide I and II regions, suggesting modifications in β-sheet crystallinity and overall molecular conformation of fibroin proteins. These structural changes likely contribute to the increased tensile properties observed in the treated silk fibers.

Importantly, the sericin content—assessed by both protein extraction and biochemical assays—did not show a significant increase or decrease compared to control groups. This consistency in fibroin-to-sericin ratio indicates that spermidine enhances silk protein synthesis in a balanced manner, avoiding overexpression of sericin which could otherwise complicate degumming and reeling processes.

The SEM micrographs supported these observations, illustrating smoother and denser silk surfaces in the polyamine-treated group, which may translate into improved tactile and mechanical performance in silk threads and fabrics. Taken together, these molecular and structural analyses confirm that polyamine supplementation not only boosts silk output but also enhances its quality at a material level.

Thus, polyamines, particularly spermidine, emerge as potent agents for improving silk fiber characteristics—offering significant potential for application in commercial sericulture.

4. IMPACT ON REPRODUCTIVE PHYSIOLOGY AND FECUNDITY

4.1 Effects on Testicular Development and Egg Production

Polyamines such as spermidine and spermine are intimately involved in reproductive physiology across a wide range of organisms, including insects. In *Bombyx mori*, the role of polyamines in gonadal development and fecundity has been extensively studied, with strong evidence pointing to their positive influence on both male and female reproductive systems.

Mysarlaet al. (2016) demonstrated that oral supplementation of fifth instar *B. mori* larvae with spermidine (50 µM) and spermine (100 µM) significantly enhanced testicular development in male moths. Treated individuals showed a marked increase in testis weight, seminiferous tubule diameter, and sperm bundle density when compared to controls. Histological sections revealed more advanced stages of spermatogenesis, suggesting that polyamines facilitate the proliferation and differentiation of germ cells within the testes.

Parallel observations were reported in females, where the same concentrations of polyamines led to increased fecundity. Females from polyamine-treated groups laid significantly more eggs than those from the control group, with an average increase of 15–25% in total egg number (Mysarlaet al., 2016). These improvements were accompanied by larger ovary size and well-developed oocytes, indicating the role of spermidine and spermine in enhancing vitellogenesis and oocyte maturation.

The authors attributed these effects to the biochemical role of polyamines in nucleic acid stabilization and protein synthesis—both critical for germ cell development. In addition, polyamines are known to modulate ion channels and signal transduction pathways, which may further support reproductive tissue growth and hormonal balance during the pre-mating period.

4.2 Reproductive Performance in Wild and Cultured Silkworms

While the reproductive benefits of polyamines have been well-documented in the domesticated *B. mori*, recent studies have extended this knowledge to wild silkworm species such as *Antheraea mylitta*. Swamy et al. (2023) evaluated the fecundity-enhancing effects of spermidine and spermine in *A. mylitta* and found similar trends to those observed in *B. mori*. When female moths were fed spermidine at concentrations of 50 µM and 100 µM, a significant increase in egg-laying capacity was observed, with a corresponding increase in hatchability.

Likewise, spermine supplementation enhanced male reproductive performance by increasing testis mass and sperm production. The reproductive success of the species was further confirmed through cross-mating experiments, which yielded higher fertilization rates and improved hatching percentages in polyamine-treated pairs (Swamy et al., 2023).

These results suggest a conserved mechanism by which polyamines enhance reproductive performance in both cultivated and wild silk moths. In both *B. mori* and *A. mylitta*, polyamine treatment appeared to synergize the processes of oogenesis and spermatogenesis, thus improving reproductive efficiency and genetic output. The observed increase in fecundity, egg viability, and reproductive tissue development emphasizes the practical value of polyamines as natural growth regulators in silkworm breeding programs.

Moreover, these findings open new avenues for the use of dietary polyamines in integrated silkworm rearing strategies, especially for improving seed stock quality in seed farms and boosting productivity in wild silk systems under semi-domesticated conditions.

5. IMPACT ACROSS SILKWORM STRAINS

5.1 Response in Parental and Hybrid Strains

The response to polyamine supplementation in *Bombyx mori* is known to vary based on genetic background, with hybrid strains frequently exhibiting superior physiological and economic traits compared to their parental lines. Recent studies have examined the effects of spermidine and spermine feeding across different silkworm strains, including both pure parental breeds and commercially important hybrids such as CSR2 × CSR4.

In a comparative study conducted by Yerra and Mamillapalli (2016), fifth instar larvae from three distinct strains—CSR2 (a bivoltine male parent), CSR4 (a bivoltine female parent), and their hybrid CSR2 × CSR4—were administered with spermidine (50 µM) and spermine (100 µM).

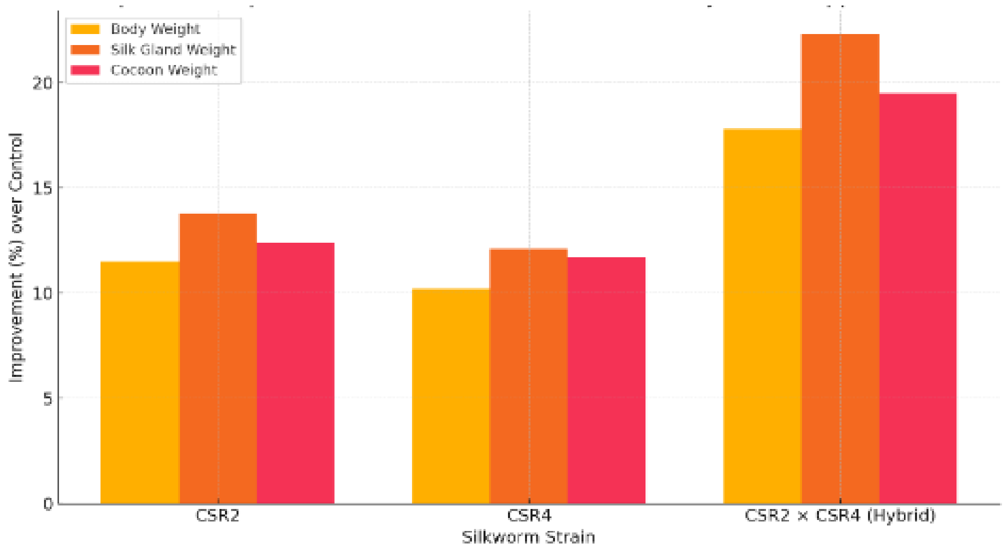

Fig. 1. The percentage improvements in body weight, silk gland weight, and cocoon weight across parental strains (CSR2, CSR4) and hybrid strain (CSR2 × CSR4) of *Bombyx mori*

Key growth and productivity parameters, including larval body weight, silk gland weight, and cocoon weight, were assessed post-treatment. The results revealed a pronounced increase in all three parameters across all strains; however, the hybrid strain CSR2 × CSR4 consistently outperformed its parental lines.

Specifically, CSR2 × CSR4 larvae treated with spermidine showed an average increase of 17.8% in larval body weight, 22.3% in silk gland weight, and 19.5% in cocoon weight compared to untreated controls. Parental strains also showed improvements, albeit to a lesser extent (Yerra & Mamillapalli, 2016). This enhancement in hybrid vigor or heterosis under polyamine influence is likely attributable to synergistic effects on metabolic pathways involved in silk protein biosynthesis and cellular energy utilization.

Furthermore, the polyamine-treated hybrids maintained superior cocoon shell ratios and filament lengths, suggesting that the enhanced physiological development translated into better silk yield and quality. Importantly, no signs of metabolic toxicity or developmental abnormalities were observed, indicating that the concentrations used were well-tolerated and biologically effective across multiple genetic lines.

The study also highlighted strain-specific sensitivity to polyamine doses. While CSR2 × CSR4 responded most positively at 50 µM spermidine and 100 µM spermine, higher or lower concentrations produced inconsistent effects in some parental lines, suggesting an optimal dose threshold that may vary depending on the genetic makeup of the strain. These findings underscore the importance of tailoring polyamine supplementation protocols to the specific genetic context of silkworm strains in order to maximize economic benefits.

Overall, the differential response of silkworm strains to polyamines not only highlights their potential as biostimulants in commercial rearing but also provides a foundation for further exploration of polyamine–genotype interactions in sericulture.

This figure shows the percentage improvements in body weight, silk gland weight, and cocoon weight across parental strains (CSR2, CSR4) and hybrid strain (CSR2 × CSR4) of *Bombyx mori* after supplementation with polyamines (spermidine and spermine). The hybrid strain shows the highest improvements, indicating enhanced responsiveness to polyamine treatment.

6. BROADER IMPLICATIONS AND APPLICATIONS

6.1 Economic and Industrial Benefits

The application of polyamines such as spermidine and spermine in sericulture has emerged as a promising strategy to enhance silk yield, quality, and overall larval health. Multiple studies have demonstrated that polyamine supplementation leads to improvements in critical parameters like larval growth, silk gland development, cocoon weight, and filament strength—all of which directly translate into increased economic returns for silk farmers and the industry.

According to Yerra et al. (2017), the dietary administration of spermidine significantly improved both the mechanical and structural properties of silk fibers, resulting in higher tensile strength and better elasticity without compromising the fibroin-to-sericin ratio. These physical enhancements are highly valuable in industrial reeling and fabric processing, as they improve reeling efficiency and final fabric quality. Additionally, the same study reported increased filament length and fiber diameter, indicating that polyamine application could help meet growing market demands for high-quality silk.

Yerra and Mamillapalli (2016) further noted that hybrid strains such as CSR2 × CSR4 showed exceptional response to polyamine supplementation, with greater improvements in cocoon and silk gland weights compared to parental strains. This suggests a scalable opportunity to integrate polyamine treatment into commercial bivoltine rearing systems, which dominate India's silk industry. The lack of toxicity and the relatively low cost of spermidine and spermine make this supplementation approach highly feasible for adoption at the grassroots level.

Given the fact that polyamines can be delivered orally via fortified mulberry leaves—without altering the core practices of rearing—this method fits seamlessly into existing sericulture operations. As a result, integrating polyamine-based formulations into standard rearing protocols could significantly boost the efficiency and sustainability of silk production, especially in developing countries where maximizing yield per unit input remains a primary goal.

6.2 Future Prospects

While current studies have firmly established the physiological benefits of polyamines in *Bombyx mori* and related species, they also point toward vast unexplored potential in the field of insect biochemistry and agricultural biotechnology. For instance, research by Chang et al. (2021) elucidated the role of spermidine in regulating the cell cycle via the upregulation of cyclin-dependent genes, revealing that polyamines influence fundamental developmental pathways that could be harnessed to optimize other economically important traits.

Furthermore, the effect of polyamines on the gut microbiome (Rajan et al., 2022) opens new frontiers in understanding host–microbe interactions in insects, with potential implications for disease resistance, digestion, and immunity. Future studies could explore polyamine metabolism under various environmental stress conditions, including heat, humidity, and pathogen exposure—factors that often compromise sericulture output.

There is also scope for the development of transgenic silkworm lines or microbial biofactories that overproduce polyamines internally, reducing the need for exogenous application. Moreover, the synergistic use of polyamines with other growth-promoting agents, such as probiotics or plant-derived elicitors, remains a largely untapped area of research.

Ultimately, advancing our understanding of polyamine biology in silkworms could lead to their broader application in other agriculturally relevant insects and animal systems, potentially revolutionizing bio-production models far beyond sericulture.

7. CONCLUSION

Polyamines, particularly spermidine and spermine have emerged as multifaceted bioactive compounds with significant potential to enhance various physiological and economic traits in silkworms (*Bombyx mori* and *Antheraea mylitta*). This review consolidates evidence from recent studies demonstrating that polyamines positively influence critical biological processes, including cell cycle progression, nutritional efficiency, silk production, and reproductive performance.

Spermidine was shown to upregulate key genes associated with DNA replication and cell cycle regulation, promoting healthy cell division in larval tissues. Simultaneously, polyamine supplementation improved food conversion efficiency and antioxidant capacity, contributing to healthier and more productive larvae. In silk production, polyamines enhanced fiber length, strength, and elasticity without disrupting the fibroin-to-sericin ratio, indicating a balanced upregulation of silk protein synthesis. Reproductively, both male and female moths benefited from optimized polyamine levels, with increased testis size, oocyte development, and fecundity documented across both parental and hybrid strains.

These benefits extend to practical applications in sericulture. Polyamine supplementation via fortified mulberry leaves is cost-effective, non-invasive, and easily integrated into existing rearing practices. Its scalability offers tremendous promise for improving the economic returns of silk farming, especially in regions reliant on sericulture for livelihood generation.

Looking ahead, further research is needed to understand the full spectrum of polyamine metabolism and its interaction with environmental and genetic factors in silkworms. Studies on transgenic approaches, microbial symbionts, and synergistic use with other biostimulants could pave the way for more sustainable and high-yielding sericulture systems. The inclusion of polyamines in routine silkworm management holds promise not just for yield enhancement, but also for promoting insect resilience and overall silk quality—an innovation with wide-reaching implications for both science and industry.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that they have no known competing financial interests or non-financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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