

# Breeding Strategies in Silkworm (*Bombyx mori*) for Environmental Adaptation: A Structured Narrative Review

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## Abstract

Climate variability increases the exposure of *Bombyx mori* to heat, humidity extremes, variable mulberry quality and pathogen pressure. The insect's long domestication history improved silk output but also narrowed genetic diversity and increased dependence on managed rearing. This structured narrative review evaluates conventional selection, hybrid breeding, marker-assisted selection, population genomics, transcriptomics and genome editing as strategies for environmental adaptation. English-language literature published from 2000 to 26 June 2026 was identified using combinations of major bibliographic databases and reference-list searches. Studies were assessed according to clarity of genetic material, stress definition, controls, replication, outcome measurement, statistical analysis and source traceability. Owing to substantial heterogeneity in strains, stress treatments and endpoints, the evidence was synthesised thematically rather than meta-analysed. Phenotypic selection and multi-environment hybrid testing remain the most deployment-ready approaches because they measure survival, productivity and silk quality simultaneously. Marker-assisted selection can accelerate introgression when loci are independently validated, whereas pan-genomic and genome-wide association resources expand the search for adaptive alleles and improve parent selection. Transcriptomics and functional studies identify heat-shock, antioxidant, immune and silk-gland pathways, but expression changes require causal validation. CRISPR-based studies have established efficient editing and produced promising antiviral and heat-resistant lines, although regulatory, pleiotropic and seed-system constraints limit immediate field deployment. The review concludes that climate-adaptive breeding should use a staged pipeline combining germplasm conservation, controlled stress screens, measured environmental covariates, cost-effective molecular support and multi-season, multi-location validation. In emerging African sericulture systems, investment in field phenotyping, parental-stock management and delivery of locally tested hybrids is as important as investment in advanced genomics.

**Keywords:** *Bombyx mori*, climate adaptation, thermotolerance, hybrid breeding, marker-assisted selection, genomics, CRISPR-Cas, genotype-by-environment interaction

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#### **Ethical approval**

The study reviewed published literature and did not involve new experiments on humans or live animals; institutional ethical approval was therefore not required.

#### **Author contributions**

J.J.K. conceptualised the review and prepared the initial manuscript. E.J.C. and P.K.K. contributed to critical interpretation, revision and supervision. All authors approved the final manuscript.

#### **Data availability**

No new dataset was generated. All evidence discussed is available in the cited publications.

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## **Introduction**

Sericulture links an agricultural production system to a high-value natural fibre industry and continues to support rural livelihoods in Asia, Africa and Latin America. Its biological centre is the domesticated silkworm, *Bombyx mori*, whose larvae convert mulberry leaves into cocoon silk. Domestication and intensive selection greatly increased silk yield, but they also narrowed the genetic base and strengthened the insect's dependence on managed environments (Goldsmith et al., 2005; Xia et al., 2014; Tong et al., 2022). This dependence has become a larger production risk as rearing regions experience more frequent heat episodes, irregular humidity and variation in mulberry quality.

Environmental adaptation in this review refers to the capacity of a silkworm genotype to maintain acceptable survival, development, cocoon yield and silk quality when exposed to non-optimal temperature, relative humidity, nutritional supply or pathogen pressure. Temperature and humidity act directly on feeding, moulting, metabolism and silk-gland activity. Experimental work has consistently shown that departures from the favourable rearing range reduce biological and economic traits, although the magnitude of loss differs among races and developmental stages (Hussain et al., 2011; Rahmathulla, 2012). Adaptation is therefore not a single trait. It is a composite outcome involving stress perception, proteostasis, antioxidant

defence, immune competence, feed conversion and preservation of silk synthesis.

Conventional breeding remains the foundation of silkworm improvement. Pure-line selection, recurrent selection, diallel or line-by-tester crossing, backcrossing and hybrid testing have generated productive bivoltine and multivoltine combinations. Their strength is that selection is based on whole-animal performance and can be conducted under the target production environment. Their weakness is that complex adaptive traits are polygenic, environmentally sensitive and sometimes negatively correlated with yield or silk quality. A line selected only under severe heat, for example, may survive stress but perform less well under favourable conditions. Multi-environment evaluation is therefore essential before deployment.

Genomic resources have changed the scale at which this problem can be addressed. The *B. mori* reference genome, high-density variation maps and the recent population-scale pan-genome have revealed extensive single-nucleotide, structural and presence-absence variation that is not captured by one reference genome (Xia et al., 2014; Tong et al., 2022). These resources support marker-assisted selection, genome-wide association studies, genomic prediction and functional validation. Recent studies have identified markers linked with thermotolerance, differentiated local germplasm across countries, and detected candidate genes associated with cocoon-producing traits (Chandrankanth et al., 2015; Xu et al., 2024; Song et al., 2025).

Functional genomics has also clarified mechanisms that can be converted into breeding targets. Heat-shock proteins, antioxidant enzymes and genes involved in energy metabolism and silk-gland function respond to thermal or oxidative stress (Li et al., 2012; Liu et al.,

2024). Genome editing is now technically efficient in *B. mori* and has been used to validate genes and create antiviral or high-temperature-resistant lines (Wang et al., 2013; Dong et al., 2019; Feng et al., 2024). However, laboratory proof of function is not equivalent to an adoptable commercial strain. Regulatory approval, off-target assessment, maintenance of silk quality, multiplication of parental stocks and the cost of diagnostic or genomic infrastructure remain major translational constraints.

Previous publications have reviewed silkworm biology, climatic management or genome editing separately. The present review integrates conventional breeding, molecular markers, population genomics, functional genomics, genome editing and genotype-by-environment evaluation within one climate-adaptation framework. It also gives particular attention to the gap between laboratory innovation and strain packages that can be used by smallholder sericulture programmes, including those emerging in Africa.

## Review Methodology

### Review Design and Scope

The study was structured narrative review rather than a meta-analysis. The purpose was to compare breeding approaches, identify consistent and conflicting evidence, and assess their readiness for use in climate-variable sericulture. A quantitative pooled effect was not calculated because the reviewed studies differed substantially in strain background, stress intensity, developmental stage, controls, outcome definitions and reporting units.

### Search Strategy

Literature searches covered January 2000 to 26 June 2026 and were undertaken using combinations of

PubMed, Scopus, Web of Science, AGRIS and Google Scholar. A representative search string was: ("*Bombyx mori*" OR silkworm) AND (breeding OR selection OR hybrid\* OR backcross\* OR "marker-assisted selection" OR QTL OR GWAS OR genomic OR transcriptom\* OR CRISPR OR "gene editing") AND (heat OR temperature OR humidity OR drought OR nutrition\* OR pathogen\* OR "environmental adaptation" OR thermotolerance). Searches were restricted to English-language records. Reference lists of relevant articles were checked to identify additional primary studies.

### Eligibility and Study Selection

Eligible records were peer-reviewed primary studies on *B. mori* that examined a breeding population, genetic resource, molecular marker, genomic association, transcriptomic response, functional gene test or genome-editing intervention relevant to environmental or biological stress. Studies of wild silkmoths were excluded unless they provided a direct comparative insight into *B. mori* domestication. Papers were also excluded when the reported article, journal or digital object identifier could not be verified. Review articles were retained only for background and method context, not as substitutes for primary evidence.

### Appraisal and Narrative Synthesis

Evidence was appraised using an adapted domain-based checklist: clarity of

the strain or population, definition and intensity of the stressor, presence of an appropriate control, biological replication, transparency of outcome measurement, adequacy of statistical analysis and traceability of the publication. Findings were grouped by breeding approach and then compared across stressors and production contexts. Greater weight was given to replicated whole-animal studies and multi-environment trials than to cell-line experiments or single-gene expression studies. Conflicting findings were interpreted in relation to genetic background, stress dose, developmental stage and rearing conditions.

### Review Limitations

The review is limited by English-language selection, uneven database indexing of sericulture journals, underrepresentation of African and Latin American field studies, and publication bias towards positive molecular findings. The heterogeneity that prevented meta-analysis also limits direct numerical comparison among approaches. These limitations are reported explicitly and are considered when recommendations are made.

## Results and Discussion

### Environmental Adaptation as a Breeding Target

**Table 1:** Environmental stress domains and breeding implications

Stress domain	Observable production effects	Priority breeding indicators	Interpretive caution
High temperature	Reduced feeding, oxidative damage, mortality, impaired cocoon and silk traits	Survival by instar; development time; cocoon weight; shell ratio; HSP/antioxidant response	Short laboratory heat shocks may not predict seasonal field performance.

Stress domain	Observable production effects	Priority breeding indicators	Interpretive caution
Humidity extremes	Dehydration at low RH; disease and moulting problems under warm, high RH	Survival; moulting success; water-loss tolerance; disease incidence	Temperature and RH should be analysed jointly.
Variable mulberry quality	Lower intake and conversion when moisture/protein decline or fibre rises	Feed conversion; larval growth; silk-gland and cocoon traits	The same genotype may respond differently to cultivar and leaf age.
Pathogen pressure	Crop loss, reduced survival and poor cocoon formation	Challenge survival; viral load; immune phenotype; fitness after infection	Resistance must not be inferred from gene expression alone.
Combined field stress	Unstable ranking of strains across sites and seasons	Mean performance, stability, G×E, economic return	Broad adaptation and specific adaptation are different breeding goals.

### Heat and Humidity Tolerance

*B. mori* is poikilothermic, and its developmental rate and survival closely track the rearing environment. Heat increases respiration and oxidative load, while low humidity accelerates water loss; the combination can impair feeding, moulting and cocoon formation. High humidity under warm conditions can create a different problem by favouring disease and disrupting evaporative balance. Hussain et al. (2011) demonstrated that temperature and humidity altered larval and cocoon traits, while Rahmathulla (2012) synthesised evidence that age-specific environmental management is necessary for stable production.

Thermotolerance is partly mediated by inducible molecular protection. Li et al. (2012) found tissue- and treatment-dependent expression of inducible heat-shock proteins, showing that HSP response is not uniform across strains or organs. More recent functional work identified *Bmsn* as a contributor to

high-temperature resistance; overexpression reduced oxidative injury and improved physiological performance under heat stress (Liu et al., 2024). Such genes are promising targets, but a single marker should not be treated as a complete predictor because survival under field conditions also depends on metabolism, feeding, humidity and disease exposure.

### Nutritional and pathogen stress

Environmental adaptation includes the ability to use variable-quality mulberry. Drought, heat, soil fertility and leaf age alter moisture, protein, fibre and secondary compounds, thereby changing the nutritional environment experienced by the larva. Breeding only for thermal survival can therefore fail if the selected genotype has poor feed conversion under stressed mulberry. Field selection should combine direct environmental stress with realistic leaf-quality variation rather than using artificial diet or optimal leaves alone.

Pathogen resistance is another component of environmental robustness because temperature, humidity and crowding modify disease risk. CRISPR-based studies have shown that host or viral genes can be manipulated to reduce *Bombyx mori* nucleopolyhedrovirus replication. Dong et al. (2019) reported substantial survival of transgenic larvae after multiplex disruption of viral immediate-early genes. Feng et al. (2024)

showed that BmSPP is a host target relevant to BmNPV resistance, and knockout animals had lower mortality than wild type. These results demonstrate biological feasibility, but commercial use requires evaluation of fitness, inheritance, biosafety and performance in standard breeding backgrounds.

### Breeding Strategies for Environmental Adaptation

**Table 2:** Representative verified evidence supporting climate-adaptive silkworm breeding

Study	Approach	Verified contribution	Implication for breeding
Hussain et al. (2011)	Controlled temperature-humidity experiment	Demonstrated significant effects of rearing environment on biological and economic traits.	Use age- and environment-specific stress screens.
Li et al. (2012)	HSP expression analysis	Showed inducible HSP responses vary by tissue and treatment.	HSPs are mechanistic candidates, not stand-alone selection criteria.
Chandrakanth et al. (2015)	Bulk-segregant analysis and SSR mapping	Identified microsatellite markers linked to thermotolerance.	Validate marker effects in independent families and environments.
Wang et al. (2013)	CRISPR/Cas genome engineering	Established efficient targeted editing in <i>B. mori</i> .	Enabled functional validation and trait engineering.
Tong et al. (2022)	Population resequencing and pan-genome	Revealed extensive structural variation and adaptive/economic trait genes.	Use diverse germplasm rather than one reference genome.
Dong et al. (2019)	Transgenic CRISPR antiviral line	Multiplex viral-gene targeting inhibited BmNPV and improved challenge survival.	Disease resistance is a realistic gene-editing application.

Study	Approach	Verified contribution	Implication for breeding
Liu et al. (2024)	Transgenic overexpression and functional assays	Confirmed a role of Bmsn in high-temperature resistance.	Functional evidence should precede marker deployment.
Xu et al. (2024)	Population genetic diversity analysis	Detected differentiation and unique diversity in Chinese and Uzbek germplasm.	Conserve geographic stocks as sources of adaptive alleles.
Song et al. (2025)	GWAS of cocoon-producing traits	Detected significant SNPs and candidate genes for cocoon traits.	Test associations under environmental stress before routine selection.
Feng et al. (2024)	CRISPR knockout and viral challenge	Identified BmSPP as a host target relevant to BmNPV resistance.	Evaluate edited resistance with fitness and production traits.

### Phenotypic Selection and Hybrid Breeding

Phenotypic selection remains the most accessible strategy for public breeding stations and smallholder-oriented programmes. Candidate lines can be exposed to target temperatures, humidity regimes or seasonally variable mulberry, followed by selection for survival, development time, cocoon weight, shell ratio and filament quality. Hybrid breeding can exploit heterosis and non-additive gene action, and field evaluations in Pakistan and India show substantial among-race and among-hybrid variation under local conditions (Bhatti et al., 2023; Hazarika et al., 2023).

The principal advantage is direct relevance to production. The same approach can also detect trade-offs that molecular screening may miss. Its disadvantages are long cycles, large rearing populations, high labour demand and confounding between genotype and environment. Selection response is strengthened when stress exposure is

standardised, parental lines are maintained carefully and performance is verified across seasons and locations. Conventional breeding is therefore not obsolete; it is the phenotypic platform on which molecular tools must be validated.

### Marker-assisted Selection and QTL Approaches

Marker-assisted selection is most useful when a reproducible marker is closely linked to a trait with moderate or large effect. Chandrakanth et al. (2015) used bulk-segregant analysis and in-silico mapping to identify microsatellite markers linked to thermotolerance. Such markers can reduce the number of animals carried to late-stage phenotyping and can support introgression into productive backgrounds. Marker-assisted selection is less effective for highly polygenic adaptation when marker effects change across environments or genetic backgrounds.

Quality control is therefore critical. A marker should be validated in independent families and target environments before routine use. Diagnostic accuracy, recombination distance, allele frequency and any association with undesirable traits should be reported. For resource-limited programmes, a small validated marker panel may be more cost-effective than whole-genome testing, but only when the panel adds predictive value beyond simple family or phenotypic information.

### Population Genomics, Pan-Genomics and Association Mapping

Population-scale genomics expands the search from a few candidate loci to the full diversity available in germplasm collections. Tong et al. (2022) resequenced 1,078 silkworms and assembled long-read genomes for 545 representatives, revealing extensive structural variation and genes associated with domestication, breeding and ecological traits. This pan-genome is important because adaptive alleles may be absent from the standard reference genome.

Regional germplasm studies provide the raw material for applied breeding. Xu et al. (2024) demonstrated genetic differentiation between Chinese and Uzbek local resources, highlighting the value of conserving geographically distinct stocks. González-Muñoz et al. (2025) similarly documented genetic and morphological variation in Colombian germplasm. Association mapping is beginning to connect this diversity to economic traits: Song et al. (2025) identified significant SNPs and candidate genes for cocoon-producing traits in four Henan strains. The next step is to test whether these associations remain predictive under heat, humidity and nutritional stress.

### Transcriptomics and Functional Validation

Transcriptomic analysis identifies pathways that respond to stress and can prioritise candidate genes, but differential expression alone does not establish causality. Heat-shock proteins, antioxidant enzymes, endoplasmic-reticulum processing and silk-protein genes repeatedly appear in stress studies. Zhou et al. (2020) showed that domestication altered co-expression networks in the silk gland and increased the capacity for fibroin synthesis. Välsalmi and Linder (2024) further linked fibroin-to-sericin composition with the extensional behaviour of silk dope, illustrating why breeding for stress survival must also preserve the physical basis of silk quality.

Functional tests are needed to separate useful regulators from secondary stress responses. Ou et al. (2025) demonstrated that BmHR3 is essential for silk-gland development and silk-protein synthesis, while Liu et al. (2024) provided direct evidence for the role of Bmsn in high-temperature resistance. Candidate prioritisation should therefore combine expression, sequence variation, physiological phenotype and evidence from gene perturbation.

### Genome editing

CRISPR-Cas systems provide efficient tools for targeted gene disruption, insertion and functional validation in *B. mori* (Wang et al., 2013; Baci et al., 2022). Antiviral applications are currently among the strongest demonstrations because target genes and challenge assays can be defined clearly. Dong et al. (2019), Liu et al. (2022) and Feng et al. (2024) each showed that editing viral or host factors can suppress BmNPV or improve survival.

For environmental adaptation, genome editing should be used cautiously. Thermotolerance is polygenic, and editing one protective gene may create

pleiotropic effects on development, reproduction or silk production. Edited lines also face regulatory and public-acceptance barriers that vary by country. Near-term value may therefore lie in functional validation and pre-breeding rather than immediate release. Before commercial deployment, edited lines require multi-generation stability tests, off-target analysis, ecological risk assessment, crossing into elite backgrounds and multi-location performance evaluation.

### **Genotype-by-environment Interaction and Deployment**

A genotype-by-environment interaction occurs when the relative ranking of strains changes among environments. This is expected in sericulture because temperature, humidity, mulberry quality and pathogen pressure vary by season and location. A line that is highly productive under controlled conditions may be unstable in a hot lowland or humid monsoon environment. Conversely, a stress-tolerant line may incur a yield penalty under optimal conditions.

Breeders should operationalise G×E analysis through a staged design. First, diverse germplasm is screened under controlled stress to remove highly susceptible material. Second, survivors are evaluated with high-quality controls to measure the cost of tolerance. Third, promising families or hybrids are tested across representative agro-ecological zones and seasons. Mixed models, AMMI or GGE biplots can then separate mean performance, stability and specific adaptation. The decision should not be whether one genotype is universally 'best', but whether the breeding programme needs a broadly adapted strain or a set of zone-specific packages.

Environmental covariates should be measured rather than represented only

by site names. Daily temperature and relative humidity, mulberry protein and fibre, disease incidence and management inputs can explain why a genotype succeeds or fails. This makes results transferable and supports prediction in new environments.

### **Translational Gap in Smallholder and African Sericulture**

The major gap is not the absence of genomic tools but the limited conversion of these tools into tested, affordable seed systems. African sericulture programmes have fewer long-term multi-location datasets and smaller breeding populations than established Asian programmes. Kenyan studies have shown that available *B. mori* strains differ in rearing and silk performance, and national initiatives have emphasised the need to select mulberry and silkworm material suited to local climates (Nguku et al., 2009; Peris et al., 2012). However, the evidence base remains too small for confident zone-specific recommendations.

A smallholder-oriented breeding strategy should prioritise traits that reduce production risk: survival, uniform development, disease resistance, acceptable shell ratio and consistent filament quality under realistic housing conditions. The most advanced technology is not always the most useful. Phenotypic selection and a few validated markers may provide greater immediate value than whole-genome prediction where genotyping costs, data management and breeding population sizes are limiting. Genomic resources remain important, but their use should be embedded in a costed delivery pathway that includes parental maintenance, egg multiplication, extension, quality control and farmer feedback.

Regulatory and biosafety systems also affect technology choice. Marker-

assisted and genomic selection use naturally occurring variation and generally face fewer barriers than transgenic or genome-edited lines. Gene editing may be appropriate for high-value traits with no

usable natural variation, but deployment decisions must account for national regulation, traceability, market acceptance and the risk of losing locally adapted diversity.

**Table 3. Comparative readiness of breeding approaches**

Approach	Strengths	Main limitations	Near-term readiness for smallholder programmes
Phenotypic selection and hybrid testing	Directly measures production; low laboratory dependence; captures whole-genome effects	Slow; labour-intensive; affected by uncontrolled environment	High, provided stress protocols and multi-site testing are standardised.
Marker-assisted selection	Early screening; useful for introgression of validated loci	Weak for highly polygenic traits; marker effects may be population-specific	Moderate to high for small validated panels.
GWAS/pan-genomics/genomic prediction	Uses genome-wide diversity; supports parent choice and complex-trait prediction	Requires large reference populations, genotyping and data capacity	Moderate for research centres; lower for routine local multiplication units.
Transcriptomics/proteomics	Reveals pathways and candidate genes	Expression may be consequence rather than cause; tissue and stage dependent	High for discovery, low as routine farmer-facing selection.
Genome editing	Direct functional test; precise modification of defined targets	Regulation, off-target risk, pleiotropy, crossing and public acceptance	Low to moderate; strongest current case is research and pre-breeding.

### **An integrated Breeding Framework**

Evidence across the reviewed studies supports an integrated rather than technology-substitution model. Conventional crossing and multi-environment phenotyping remain

indispensable, while molecular tools improve parent choice, early screening and understanding of mechanism. A practical pipeline begins with germplasm conservation and characterisation, proceeds through controlled and field

stress phenotyping, uses markers or genomic information where they demonstrably improve prediction, and ends with multi-season validation and seed-system planning.

Breeding objectives should be defined as multi-trait indices. Survival alone is insufficient if cocoon quality declines; cocoon weight alone is insufficient if development becomes too long or disease susceptibility rises. Indices should include survival, larval duration, cocoon weight, shell percentage, filament traits, fecundity and stability across environments. Where molecular data are

available, markers should complement rather than replace these phenotypes.

Economic evaluation should be included early. The cost per selected family, genotyping turnaround time, infrastructure requirements and expected reduction in crop failure determine whether an approach is scalable. For smallholder systems, the most defensible pathway is usually a tiered programme: low-cost phenotypic screening for the whole population, targeted genotyping of elite families and intensive genomic or transcriptomic analysis only for final candidates or unresolved traits.

**Table 4:** Staged breeding and deployment pipeline

Stage	Core activity	Decision criterion	Output
1. Germplasm assembly	Collect local, improved and exotic lines; verify identity and health	Adequate genetic and geographic diversity	Curated breeding population
2. Controlled screening	Expose families to defined heat, humidity, nutrition or pathogen challenges	Survival with acceptable growth and silk traits	Stress-tolerant candidates
3. Molecular support	Apply validated markers or genome-wide data to elite families	Improved prediction beyond phenotype alone	Reduced candidate set and informed crosses
4. Multi-environment testing	Evaluate across representative zones, seasons and management levels	Mean performance, stability and manageable trade-offs	Broadly or specifically adapted hybrids
5. Economic and regulatory assessment	Estimate selection cost, multiplication feasibility and compliance needs	Benefit exceeds cost; acceptable risk and regulation	Deployment recommendation
6. Seed-system validation	Multiply parental lines and test farmer-level performance	Genetic purity and consistent field performance	Release and extension package

## Conclusions

Environmental adaptation in *B. mori* is a complex, multi-trait breeding problem. Conventional selection and hybridisation remain the most deployment-ready approaches because they measure whole-animal performance in the target environment. Marker-assisted selection can accelerate introgression when markers are validated, while pan-genomics, diversity studies and GWAS broaden the pool of candidate alleles. Transcriptomics and genome editing are powerful for discovering and confirming mechanisms, but their commercial value depends on preservation of silk quality, regulatory acceptance and successful transfer into elite breeding backgrounds.

The most important future direction is systematic integration. Breeding programmes should combine conserved germplasm, controlled stress screens, realistic multi-location trials, measured environmental covariates and cost-effective molecular tools. This approach can distinguish broad adaptation from specific adaptation, expose trade-offs and generate strain packages suited to particular agro-ecological zones. For emerging sericulture regions, especially in Africa, investment in field phenotyping, breeding populations and seed delivery is as important as investment in genomics.

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