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A review on heat stress altering the insect life history strategies and underlying mechanisms: Special reference to an economically important Lepidoptera, *Bombyx mori* (Linnaeus, 1758) (Lepidoptera: Bombycidae)

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Abstract

Lepidoptera is an order belonging to class Insecta consisting of Rhopalocera and Heterocera. *B. mori* belongs to this order and is the backbone of sericulture. Sericulture, the culture, rearing and maintenance of *Bombyx mori* (Linnaeus, 1785) for silk production, is widely practiced in India, contributing to its economy and providing livelihoods to many, especially those from lower socioeconomic backgrounds. Temperature and humidity affect silk production greatly. Heat shock genes and proteins protect *B. mori* to a certain extent from increased heat stress. However, outside this range, silkworm biology suffers. The silkworm adapts to heat by upregulating thermotolerance genes and proteins, especially heat shock proteins (HSPs). Produce different heat-resistant proteins at different temperatures. Larvae, embryos, and cocoons are affected by heat stress. Given the silkworm's sensitivity to temperature and humidity and the alarming pace of climate change and global warming faced by the earth, it is necessary to consider solutions that will allow *B. mori* to adapt in the future decades. Molecular and enzymatic markers may help screen thermotolerant silkworm breeds. Given this insect's temperature sensitivity, global warming and climate change may harm it even more than other insects. Therefore, to save this insect and the sericulture sector, steps must be taken in this direction.

Keywords: Lepidoptera, Bombycidae, thermo-tolerance, Heat shock proteins, biomarkers, global warming.

Una revisión sobre el estrés térmico que altera las estrategias vitales de los insectos y los mecanismos subyacentes: Especial referencia a un Lepidoptera de importancia económica, *Bombyx mori* (Linnaeus, 1758) (Lepidoptera: Bombycidae)

Resumen

Lepidoptera es un orden perteneciente a la clase Insecta que consiste en Rhopalocera y Heterocera. *B. mori* pertenece a este orden y es la columna vertebral de la sericultura. La sericultura, el cultivo, la cría y el mantenimiento de *Bombyx mori* (Linnaeus, 1785) para la producción de seda, se practica ampliamente en la India, lo que contribuye a su economía y proporciona medios de subsistencia a muchos, especialmente a aquellos de entornos socioeconómicos más bajos. La temperatura y la humedad afectan en gran medida la producción de seda. Los genes y proteínas de choque térmico protegen a los gusanos de seda hasta cierto punto del aumento del estrés por calor. Sin embargo, fuera de este rango, la biología del gusano de seda sufre. El gusano de seda se adapta al calor regulando al alza los genes y las proteínas de termotolerancia, especialmente las proteínas de choque térmico (HSP). Los gusanos de seda producen diferentes proteínas resistentes al calor a diferentes temperaturas. Las larvas, los embriones y los capullos se ven afectados por el estrés por calor. Dada la sensibilidad del gusano de seda a la temperatura y la humedad y el ritmo alarmante del cambio climático y el calentamiento global que enfrenta la tierra, es necesario considerar soluciones que permitan a *B. mori* adaptarse en las próximas décadas. Los marcadores moleculares y enzimáticos pueden ayudar a detectar razas de gusanos de seda termotolerantes. Dada la sensibilidad a la temperatura de este insecto, el calentamiento global y el cambio climático pueden dañarlo incluso más que a otros insectos. Por lo tanto, para salvar a este insecto y al sector de la sericultura, se deben tomar medidas en esta dirección.

Palabras clave: Lepidoptera, Bombycidae, termo-tolerancia, proteínas de choque térmico, biomarcadores, calentamiento global.

Introduction

Lepidoptera belongs to the Class Insecta which is the second-largest order of this order. It includes Heterocera and Rhopalocera. According to a recent study, 157,424 Lepidopteran species have been reported globally belonging to 124 families (van Nieukerken et al. 2011). Moths are agricultural pests, food for birds, bats, and insects, and night pollinators. Lepidoptera, being closely related with their surroundings, can be employed as ecological indicators to monitor destruction of the environment (Dar & Jamal, 2021a; Dar et al. 2022; Sheikh et al. 2022). They serve as research models for biodiversity conservation, evolution, genetics, ethology, and genetics (Samways, 2007). *Bombyx mori* (Linnaeus, 1758), also known as the silkworm, is a Lepidoptera insect that is used for producing silk and is the backbone of the silk industry. During its larval stage, *B. mori* consumes exclusively mulberry leaves as its sole food source. Sericulture is the rearing of *B. mori* for the production of silk. It is mainly practiced in China and India’s northern and southern belts, with the northern region producing bivoltine silk from bivoltine *B. mori* that are only suitable for temperate climates (Rathnam et al. 2013). Although the southern belt produces most of India’s silk, it mainly relies on multivoltine sericulture, which is based on the culture of multivoltine *B. mori* (Taufique et al. 2021). Multivoltine *B. mori* are hardy and temperature tolerant than bivoltine *B. mori*.

Looking at the current situation on a worldwide scale, we are confronted with climate change and global warming concerns. Extreme weather events, such as increased forest fires, increased precipitation, and higher temperatures, are a noticeable result of these worldwide (Frame et al. 2020). Climate change has already started to affect some insect populations, like moths, whose population has declined a lot, and climate change has played a considerable part in this decline (Dar & Jamal, 2021b). We are seeing more of these unusual occurrences these days. When we consider the worldwide scenario, it can readily be concluded that global warming is progressing at an alarming rate and will continue to do so in the following decades. As a result, a study of the effects of global warming on “life on Earth” is required.

Given that *B. mori* is particularly sensitive to the temperature fluctuations of its surroundings, we have addressed the topic of global warming and climate change concerning *B. mori* and the mulberry sericulture sector in India in this review. This review also summarizes the effects of high temperatures on the biology and economic characteristics of the silkworm *B. mori*. We also detail the proteins and genes involved in these worms’ thermotolerance and supplement previously published reviews with new data.

Heat stress effects on *B. mori* biology

B. mori life cycle and general biology are greatly dependent on the environment it grows in. Some breeds are naturally more tolerant to temperature and other abiotic stresses (Kumaresan et al. 2012). Some Indian indigenous silkworm breeds can tolerate the temperature extreme of up to 32ºC e.g., Nistari breed of *B. mori* has a pupation percentage, which is indicative of a measure of thermotolerance, of 84% and 80% in unfavourable wet summer and dry summer respectively compared to 94% in favourable season (October-March) (Moorthy et al. 2007). An increase in temperature harms *B. mori* e.g., hatchability of eggs in Nistari breed dropped to zero under a stress of 43ºC (Sinha & Sanyal, 2013). A crossbreed of *B. mori* (PM X CSR2) when kept at 30ºC and 40ºC in lab setting didn’t lay eggs at 30ºC and died at 40ºC (Wanule & Balkhande, 2013). Thermal stress also leads to oxidative damage in the body of *B. mori* as was studied in Polyvoltine (Nistari and Sarupat) and bivoltine (SK6 and SK7) by exposing them to temperatures of 35ºC and 40ºC (Makwana et al. 2021).

To successfully breed *B. mori*, temperature and humidity play the most crucial role. An increase in ambient temperature causes adverse effects on average growth and development and also affects the cocoon characters. Cocoon weight is highest when *B. mori* (Pure Mysore and NB4D2) is cultured at 25^{o}C and with the increase in temperature the cocoon weight decreases (Khan, 2014). Tanjung et al. (2017) found that heat stress given to *B. mori* larva (C301 strain) for a brief period (3 hours in the IVth instar) accelerates its larval stages thereby directly affecting the larval development thus, reducing productivity. Different instars of *B. mori* larvae tolerate and respond to thermal stress differently. Studies on some strains of silkworm (NB4D2, NP2, CSR2, KSO1and CSR4), showed resistance to heat shock (35ºC, 40ºC, and 45ºC for 2 hours), increased with larval development from Ist instar to Vth instar with Ist, IInd and IIIrd instars of NB4D2, NP2, CSR2, KSO1and CSR4 being more sensitive to high temperatures of 35ºC and 40ºC than IVth and Vth instars (Chavadi et al. 2006). However, the study also showed that heat shock affects the effective rearing rate (ERR) at a higher temperature and increases the cocoon and shell weight (Chavadi et al. 2006). High temperature affects silkworm not only in the larval stages but also in the embryonic stages. When exposed to high temperatures (40oC for 2 hours), Eggs significantly reduced their hatching percentage in a study (Taha, 2013). A decrease in fecundity was also observed when the silkworm breed (CSR18) was reared above 42ºC. Temperature above 42ºC greatly affects the development of ovaries and reproductive performance in adult moths of *B. mori* (Paul & Keshan, 2016). The impact of high temperature is not only limited to silkworm economic characteristics or health of *B. mori,* but it has also been found that high temperature affects the gut flora of silkworm (Diazo strain), decreasing the abundance of the flora as the temperature rises (Sun et al. 2017).

B. mori, has different breeds, and all of them don't behave similarly. Some are more sensitive to environmental stresses than others. Thiagarajan et al. (1993) evaluated some breeds of *B. mori* for their season-specific variation. They selected those that performed well in particular seasons (European, 14M for spring, JC2P for summer, and M2 for autumn performed well for most of the characters selected). Lakshmi et al. (2012) showed the difficulty in a culture of bivoltine breeds in tropical environments of West Bengal. The increased temperatures of the tropics directly affected and decreased the quantitative characteristics like viability and cocoon quality of bivoltine silkworm thus making it difficult for commercial breeding of bivoltine *B. mori* in those areas. High temperature also harms the larval survival rate apart from reducing cocoon and shell weight (Kato et al. 1998). The extreme sensitivity of *B. mori* to heat stress makes it imperative to grow in a particular range of temperatures successfully and comfortably. A temperature falling between 20ºC and 28ºC is optimum for bivoltine silkworm culture. However, for better productivity temperature range from 23ºC to 28ºC proves lucrative for this industry. A rise in temperature above 30ºC or a drop in temperature below 20^{o}C both prove detrimental to *B. mori,* affecting their health and making them susceptible to diseases. Both these factors are directly proportional to loss in productivity (Rahmathulla et al. 2012).

Kumar et al. (2001) found that Silkworm hybrids (F1) between a polyvoltine (Mori breed) and bivoltine races (N137, C146) are more thermotolerant than pure breeds. It was also observed that "maternal effect" also has a role to play in thermotolerance, because of the increased performance and thermotolerance of those hybrids where female parent used, was more thermotolerant. The increased better performance was seen in characteristics like pupation rate, cocoon weight, shell weight, and shell ratio. However, overall, the performance decreased as the larvae were exposed to 48ºC continuously, indicating a specific limit of thermotolerance for heat stress. The fact that *B. mori* can tolerate only a narrow range of temperatures and an increase in temperature directly affects the biology of *B. mori*, having effects on cocoon characters, larval development, etc. can be exploited to screen thermotolerant silkworm breeds as was demonstrated in a study by Chandrakanth et al. (2015) by selection of bivoltine breeds based on their pupation percentage after exposing to temperatures of 20ºC, 32ºC, 34ºC, and 36ºC. Based on their evaluation, SK4C and BHR3 were thermotolerant bivoltine breeds out of 20 selected initially in their study. *B. mori,* under lab conditions, was exposed to different stress like starvation, cold, and heat stress, and their combination affected its thermal tolerance in different ways. Starvation on the one hand improved cold tolerance but decreased heat tolerance, indicating trade-offs between these two stresses (Mir & Qamar, 2018). It is evident from the literature that thermal stress harms *B. mori* biology. However, to negate and protect its body from thermal stress up to a certain level, the body of a silkworm responds to heat stress *via* the expression of a particular class of proteins called heat shock proteins (HSP). Figure 1 summarises the negative effects of heat shock on *Bombyx mori* in general.

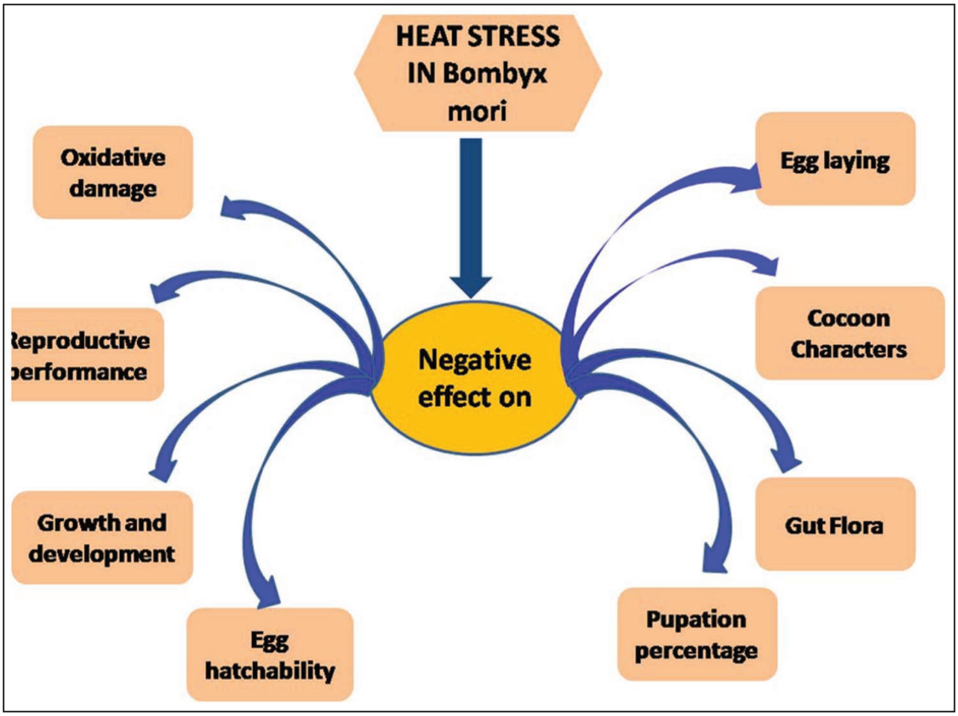

Figure 1. Summarization of negative effects of heat stress on *B. mori.* Heat stress negatively affects various parameters like egg laying, Cocoon characters, Gut flora, Pupation percentage, Egg hatchability, Growth and development, Reproductive performance and also leads to oxidative damage.

Proteins involved in thermotolerance of *B. mori*

Response to heat shock in the silkworm body is led by heat shock proteins (HSPs) which are expressed in response to heat shock in each organ of silkworm body. Heat shock proteins (HSPs) are a family of proteins that are evolutionary conserved, increasing their expression in an organism's body to varied environmental insults (Kundapur et al. 2009). Another class of heat shock proteins namely small heat shock proteins (sHSPs) play a crucial part in the control of a variety of biological processes, including temperature stress, abiotic stress, immunological responses, metamorphosis, and embryo development. sHSPs are conserved among insects (Liu et al. 2018). Silkworm strains including multivoltine (KNT, CFP, GCM, CLPF, GLPF, PAF, GFP-C, AP-White, ISK, CDFP, IIA, GDFP) and bivoltine silkworm strains (BD2S, BO2, SOF-Br, BO1S, BO1N, SOC-B, BO3BL) when given heat stress (40ºC and 45ºC for 1 hour) and subsequent analysis of protein content in the haemolymph of treated and control done, revealed that protein content in haemolymph increased many folds compared to control (Kumari et al. 2020). An increase in protein content in haemolymph may be due to an increase in the level of heat shock proteins. With temperature shock, every silkworm strain/breed responds by increasing the expression of heat shock proteins. However different strains/breeds or races express these heat shock proteins (HSPs) with some variations. A different set of heat shock proteins expressed in different strains in response to heat stress makes them able to tolerate the rise in temperature to a few degrees. However, there is a limit to the thermal tolerance of silkworm races. Different researchers have worked to elucidate the foreplay of proteins involved in the heat stress of *B. mori*. Joy et al. (1995) studied the heat shock response of multivoltine silkworm strains (*C. Nichi* and *Pure Mysore*) and a bivoltine strain (NB4D2) and observed the consequent appearance of a 93KDa protein (HSP) to heat shock in fat body, cuticle and haemolymph in both multivoltine and bivoltine breeds of silkworm, however, with a slight difference in timing of their appearances. Another protein (HSP) having a molecular mass of 70kDa was found to be present, however, constitutively in fat body and cuticle of all the strains under study (*C. Nichi, Pure Mysore* and NB4D2). Li et al. (2012) explored proteomic analysis of the posterior silk gland of hybrid silkworm strains (Qiufeng x Baiyu) and its parents, Qiufeng and Baiyu, under high-temperature treatment (42^{o}C for varied periods ranging from 10 min to 3 days) and found temperature stress induces expression of small heat shock proteins (sHSP) viz. hsp20.4, hsp20.8, alpha-crystallin. Proteome analysis done via peptide mass fingerprinting revealed this information. Thermotolerance was more in hybrids (Qiufeng x Baiyu) compared to their parents (Qiufeng and Baiyu) as was evident from the higher upregulation of proteins involved in heat stress in hybrids compared to parents. Heat greatly affected the silk synthesis as protein involved in silk metabolism identified in posterior silk gland viz adenosine kinase (ADK), ribosomal protein P0, P2, elongation factor 1b' (EF-1b'), EF-1 delta and fibroin L-chain were affected with heat stress and its effects were more pronounced in hybrids where they got down-regulated than parents indicating that hybrids although more tolerant to heat stress, however, are more prone to receive effect on silk production by heat stress. Kundapur et al. (2009) compared protein expression in silk gland of normal and heat-shocked bivoltine silkworm strains (NB4D2) and found that SDS-PAGE of heat shock treatment of silkworm had 29 proteins overexpressed compared to control silkworm indicating silk glands produce heat shock proteins in response to heat stress thus protecting its physiology. Howrelia et al. (2011) studied the effect of temperature treatment (38ºC and 42ºC for 3 hr followed by 3 hr recovery) on the heat shock protein expression of *B. mori* cross breed (multivoltine PM x CSR2 bivoltine). SDS-PAGE analysis revealed the expression of eight protein polypeptides (119 kDa, 90 kDa, 67 kDa, 49 kDa, 43 kDa, 39 kDa, 27 kDa, and 25 kDa) in hemolymph in the IVth instar. When compared between IVth and Vth instars, down-regulation of protein profiles of Vth instar larvae in response to elevated heat shock conditions was seen. However, the eight identified proteins in hemolymph showed no change in expression with respect to heat stress. In the Vth instar, the expression of 90kDa protein was down-regulated but very pronounced in the IVth instar hemolymph of the silkworm. Heat shock at different temperatures also induced expression of proteins in the fat body, with molecular mass of 90 kDa, 73 kDa, 65 kDa, 44 kDa, 37 kDa, 22 kDa, and 18 kDa were observed in IVth instar in *B. mori* cross breed PM x CSR2. The increase in resistance to heat shock was directly proportional to the increase in larval development, which was achieved by the induction of HSP 72 in the haemolymph of Vth instar larvae.

Some strains are acclimatized to the higher temperatures as is the case with the indigenous Nistari breed of the silkworm. This multivoltine breed shows late-stage larvae exhibiting more tolerance than adult moths and eggs. The temperature of 43ºC was lethal to eggs, larvae, and adults. However, the temperature of 33ºC was tolerated well. When given, heat stress (17ºC, 33ºC, and 43ºC for 3 consecutive days with a 1-hour duration) affects the HSPs in hemolymph, with the kinetics of 72kDa being different in IVth and Vth instars. There is an increased appearance of 95kDa protein in Vth instar consequent to heat shock, as was revealed by SDS-PAGE). Heat shock proteins provide it enough thermotolerance to survive the high ambient temperature of its surroundings (Sinha et al. 2013). Sinha et al. (2013) also studied the persistence of 72KDa in hemolymph in IV^th^ instar of Nistari after exposure to 43ºC and its absence in hemolymph after 17ºC and 33ºC temperature treatment. This indicated the role of HSP 72 in facilitating breed Nistari silkworm larvae with thermotolerance against heat shock. V^th^ instar larval hemolymph, however, expressed 72kDa protein constitutively. When given heat shock, its expression increased, thus proving the different behavior of silkworm larvae in terms of HSP expression in different stages. This also explains the phenomenon of higher temperature tolerance in late-age *B. mori*. Exposure of bivoltine silkworm (strain p50) eggs to 40ºC for 4 hours increased levels of 70kDa and 27kDa and increased tolerance to heat shock in larval stages. Exposure to 48ºC proved to be lethal. However, exposure to 10ºC lowered heat tolerance and did not affect 70kDa and 27kDa protein levels. Increased hardening of eggs at mild temperatures increased heat tolerance in subsequent larval stages. The importance of 70kDa and 27kDa in the thermotolerance of silkworm eggs (strain p50) was revealed (Matsuoka et al. 2018). In another study, the effect of mild heat shock treatment of silkworm strains (CSR2 and CSR4) at 30ºC for 1 hour at blastokinesis stage proved beneficial for hatching, (97%). Heat shock treatment above 45ºC was lethal, reducing the hatching percentage to below 50%. SDS-PAGE revealed overexpression of 30kDa in a 3-day embryo at 30ºC heat shock. Some protein synthesis got inhibited at and above 45ºC (84kDa, 49kDa, 22kDa, and 21kDa) in the 4-day-old embryo. Late embryonic stages are thermotolerant than early embryonic staged up to blastokinesis (Manjunatha et al. 2007). Heat stress (27ºC or 35ºC for 18 h,) has also been found to have negative effects on the important metabolic pathways of bivoltine silkworm (strain 932 and HY) like glucose metabolism, lipid metabolism, and oxidative phosphorylation and during early continuous heat stress, several heat shock proteins (HSPs) are upregulated viz. HSP19.9, HSP23.7, HSP40-3, HSP70, HSP90 and HSP70 (Li et al. 2014). *B. mori* heat shock proteins, Bmhsp 19.9 got overexpressed in bmE cell line of *B. mori* upon challenged with BmNPV (*B. mori* nuclear polyhydrosis virus) and high temperature thereby protecting bmE cells against BmNPV infection (Jiang et al. 2021). Sosalegowda et al. (2010) analysed and identified heat shock proteins in 70 tropical bivoltine and polyvoltine strains of silkworm and found the expression of 90kDa HSP in the I^st^, II^nd^ and III^rd^ instars and the expression of 84kDa HSP in IV^th^ instars. However, other HSPs like 90kDa, 84 kDa, 62 kDa, 60 kDa, 52 kDa, and 33 kDa HSP were predominantly found in V^th^ instars. Literature is rife with the upfront role of heat shock proteins in thermotolerance, but another class of heat shock proteins, namely small heat shock proteins (sHSP) have also been found to play their part in thermotolerances of *B. mori*. *B. mori* has the greatest number of insect small heat shock proteins (sHSP) characterized among class insects. 16 sHSP genes have been identified by the genome-wide analysis, which is the most among insects (Li et al. 2009). In p50 strain of silkworm, cDNAs encoding sHSPs viz. sHsp19.9, sHsp20.1, sHsp20.4, sHsp20.8, sHsp21.4, sHsp23.7 and sHSP 21.4 were isolated. A substantial increase in the transcript level of sHSPs was seen after a heat shock, except for sHSP 21.4. The study revealed the role of small heat shock proteins (sHSP) in heat shock. Also, it gave an idea about the groups of heat shock proteins operation in *B. mori* body (p50 strain). It was inferred that possibly two classes of small heat shock proteins are involved in giving heat shock resistance to silkworm, one being sHSP 21.4 and the other the larger group including the mentioned sHSPs (sHSPs viz. sHsp19.9, sHsp20.1, sHsp20.4, sHsp20.8, sHsp21.4, sHsp23.7) (Sakano et al. 2006). Downregulation of HSP 70 and upregulation of small heat shock proteins (sHSP) viz sHSP 19.9 and sHSP 20.4 was seen in Nistari and jingsong strain under temperature stress of 41ºC and 45ºC for 1 to 2 hours (Li et al. 2012). In another study, the expressions of HSP70-1, HSP70-2, and HSP70-3 were upregulated in response to thermal (37ºC and 42ºC) and cold (2ºC) stressors. (Fang et al. 2021). Table1 summarises the different proteins (heat shock proteins) involved in thermotolerance in different tissues and different life stages of different silkworm, *B. mori* strains. The involvement of heat shock proteins in thermotolerance is a phenomenon found in most organisms. Table 2 briefly summarizes the different heat shock proteins involved in temperature tolerance in organisms other than.

Table 1. Different heat shock proteins involved in thermotolerance of different silkworm breeds of *Bombyx mori* and their location/stage of life cycle.

***Bombyx mori* (breed/strain)**	**Heat shock proteins(HSP) involved in thermotolerance**	**Organ of body of stage of life cycle**
C. Nichi, Pure Mysore, NB4D2	93kDA, 70 kDA	Fat body, Cuticle and hemolymph.
PMxCSR2	119 kDA, 72 kDA,90 kDA, 67 kDA, 49 kDA, 43 kDA, 39 kDA, 27 kDA, 25 kDA	Hemolymph
PMxCSR2	73 kDA, 65 kDA, 44 kDA, 37 kDA, 22 kDA, 18 kDA.	Fat body
Nistari	72 kDA, 95 kDA	Hemolymph
P50	70 kDA, 27 kDA,	Egg
CSR2	30 kDA, 84 kDA,	Embryo
CSR4	49 kDA, 22 kDA, 21 kDA	Embryo
	Small Heat Shock Proteins (sHSP)	
***Bombyx mori* (breed/strain)**	**Heat shock proteins(HSP) involved in thermotolerance**	**Organ of body of stage of life cycle**
932 and HY	19.9 kDA. 23.7 kDA,	Midgut
Qiufeng x Baiyu, Qiufeng and Baiyu.	20.4 kDA, 20.8 kDA, alpha crystalin	Posterior silk gland
Jingsong and Nistari	19.9 kDA and 20.4 kDA	Fat body, testis and ovary

Table 2. Involvement of different heat shock proteins (HSPs) for heat tolerance in different organisms.

Organism	**Heat shock protein (HSP)**	**Role played in the organism**	**Reference**
Drosophila subobscura	HSP 70	Thermotolerance	Calabria et al. 2012
Drosophila melanogaster	HSP 70, HSP 22	Thermotolerance	Shilova et al. 2020
Brachionus manjavacas	HSP40, *HSP60, HSP70,*	Thermotolerance and survival after heat shock	Smith et al. 2012
Livestock	HSP70, HSP90 and HSP27 a	Protective role during heat stress	Archana et al. 2017
Leishmania donovani	23 kDA HSP	Prevention from heat stress	Hombach et al. 2014
Tharparkar cattle	HSP 70	Thermotolerance	Bhat et al. 2016
Italian Holstein cows	Hsp70.1	Different cellular stresses	Basiricò et al. 2011
Laodelphax striatellus	LSHSP20.1, LSHSP21.2, LSHSP21.4, and *LSHSP22.0*)	Heat stress tolerance	Wang et al. 2019
amphipods	Hsp 70	Thermotolerance	Shatilina et al. 2011
Domestic Ruminants	HSP60, 70, 90, 110, 27	Thermotolerance	Hyder et al. 2017
Bemisia tabaci	hsp40, hsp70, and hsp90	Temperature stress	Jiang et al. 2017
Frankliniella occidentalis	HSP70s	Thermotolerance	Jing et al. 2018
Colorado potato beetle	Hsp70	Thermotolerance	Chen et al. 2016
Ectomyelois ceratoniae	HSP70 and HSP90	Heat and cold tolerance	Farahani et al. 2020

Genetics of thermotolerance in *B. mori*

Upon a temperature rise, the level of heat shock proteins (HSP) increases automatically in different tissues of the *B. mori*. All this is governed by the foreplay of gene expression in the background. Studies have found that, apart from normal gene expression of HSP genes in response to heat stress, epigenetics also plays a role in thermotolerance in *B. mori* (Knobbed & 7532). A study about comparative analysis of DNA methylation profiles between these two silkworm strains of different heat tolerances via whole genome bisulfite sequencing (WGBS) revealed the involvement of 10 DMG (DMR-related genes) in heat-humidity stress, indicating the role of DNA methylation in response to silkworm to environmental insults (Chen et al. 2020). Transcriptome profiling analysis of the same silkworm strains (KNOBBED and 7532) when done at continuous high-temperature treatment (6h, 24h, 48h) and then compared, a total of 4944 differentially expressed genes (DEGs) were identified. 12 DEGs were found to have their contributions in heat-humidity stress. Four genes, BGIBMGA003739, BGIBMGA005876, BGIBMGA011821, and Novel01749, were differentially expressed between the two strains at all time points (Xiao et al. 2017). In another study, it was found that the expression of HSP90 and HSP70 genes almost always got upregulated during heat stress (45ºC for 35 min) in *B. mori* {(103 x 104 and 107 x 110) & (110 x 107 and 104 x 103)} (Mousavi et al. 2017). Wang et al. 2014 found BmHsp (*B. mori* heat shock protein) 27.4 gene has an important role in high-temperature heat stress in silkworm (variety 7532). BmHsp 27.4 gene was found on chromosome number 5 with an open reading frame (ORF) of 741 bp and expressed in fat bodies, brain and eyes. Moreover, its mRNA expression was found to increase with increasing temperature. Ubiquitous expression of HSP 90 mRNA in almost all tissues, viz. wing disc and dorsal abdominal epidermis during the larval stage, and fat body and ovary during the pupal stage is seen in the *B. mori*. At mild stress (39ºC and 42ºC), the expression of HSP 90 increases with heat stress. However, the expression level was found to change within the different organs under study. When the temperature reaches the severe category or lethal category (45ºC), the expression HSP 90 is stopped indicating the vital role of HSP 90 in the thermotolerance of *B. mori* (Keshan et al. 2014). Heat stress in DZ-37 breed affects genes involved in the immune system, like BmRel and BmSerpin-2, downregulating them and thus making the silkworm prone to infections (Guo et al. 2018).

Climate change and the silk industry

Climate change, which is the result of “Global Warming” or a rise in global temperature, is currently impacting worldwide. The increase in concentrations of greenhouse gases (GHGs) such as carbon dioxide (CO2), methane (CH4), and nitrous oxide (NOx) is primarily responsible for the rise in global atmospheric temperature. The combustion of fossil fuels, fast industrialization, deforestation, agricultural operations, luxury/modernization of living style (home appliances), space explosion, grazing, wetland degradation, and land use change are all linked to increased GHG emissions (Figure 2) (Ram et al. 2016). Global warming has wreaked havoc in 2022 alone, causing forest fires, droughts, flooding, and other natural disasters. Forest fires in Europe have caused chaos on a significant expanse, claimed lives, destroyed property worth millions, and destroyed the habitat of numerous kinds of organisms that had been living there (https://www.theguardian.com/environment/2022/aug/08/the-new-normal-how-europe-is-being-hit-by-a-climate-driven-drought-crisis). Wildfires in the south of France have destroyed an area equal to 22000 acres (https://www.nytimes.com/2022/07/16/world/europe/uk-europe-heat-wave.html). A record-breaking heat wave that affected much of Europe started the wildfires. Throughout just 2022, 1.27 million acres of land burnt in Europe. (https://www.theguardian.com/environment/ng-interactive/2022/jul/26/how-europe-has-been-hit-by-record-fire-damage-and-temperatures). A record heat wave with temperatures reaching 50 C occurred in India and Pakistan due to climate change in south-east Asia. This unusually sweltering heat wave, made 30 times more likely by global warming, was a direct outcome of climate change and impacted crops like maize and farmers’ output. (https://www.theguardian.com/environment/2022/may/23/deadly-indian-heatwave-made-30-times-more-likely-by-climate-crisis). An unprecedented record monsoon downpour in Pakistan produced massive flooding that submerged 1/3 of the country, killed many people, destroyed vast amounts of property, and damaged critical infrastructure, bringing agony to the people there. (https://www.theguardian.com/commentisfree/2022/aug/29/the-guardian-view-on-climate-chaos-in-pakistan-adapt-to-survive). The root cause of all these catastrophic events in one, climate change.

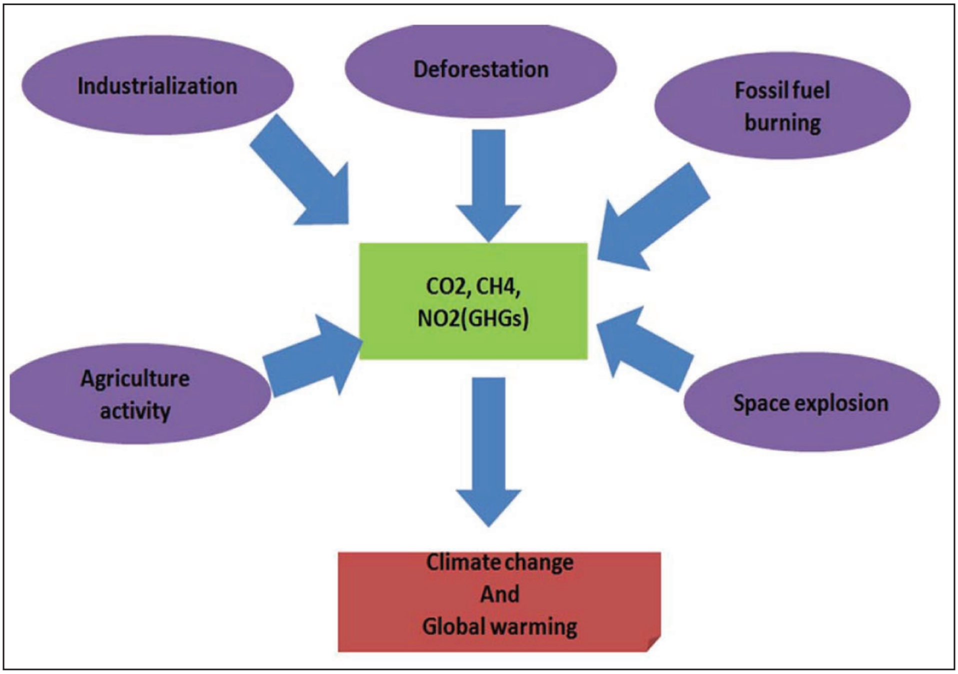

Figure 2. Activities leading to increase in greenhouse gasses (GHGs) viz., CO_2, CH_4, NO_2 which in-turn lead to climate change and global warming.

Because life on Earth is inextricably linked to the climate, every change in it impacts all forms of life. Climate change is the key predictor of agricultural productivity, which directly impacts global food production (Malini et al. 2018). The maximum temperature in India has risen during the previous century, with varying degrees of growth in different parts of the country. The maximum temperature on India's west coast increased by about 1.2ºC, in the northeast by about 1ºC, in the Western Himalayas by about 0.9ºC, in the north central by about 0.8ºC, in the northwest by about 0.6C, and on the east coast by about 0.6ºC (Dash et al. 2007). Using different climate models, scientists have predicted a temperature increase of 4.0ºC to 5.8ºC in the next few decades (Chauhan et al. 2014). IPCC (Intergovernmental panel on climate change) reported global warming of 1.4^{o}C to 5.6^{o}C by 2100 (Sathaye et al. 2006). With the rapid and threatening pace of climate change and warming, some scientists believe that keeping the global rise in temperature below 2ºC seems complicated (Peters et al. 2013). A surge in 2ºC and its effects could be unpleasant, but some studies estimate that at the end of the 21st century, a global rise of 4^{o}C is also possible, which could be simply disastrous (Betts et al. 2011). A consensus between different studies implies a global rise in temperatures greater than 2ºC before the start of the next century.

Although climate change harms all life, here we will focus on insects in general and *B. mori* in particular. Insects and the ecosystems they depend on are at risk due to climate change, whether they are terrestrial (Burrows et al. 2011), freshwater (Woodward et al. 2010), or subterranean (Mammola et al. 2019). When we consider the overall picture of insect extinctions, we lose a lot more than simply species. Insect diversity, abundance, and biomass are lost over large networks of biotic interactions, as well as significant chunks of the tree of life, unique ecological features, and ecological functions. As a result of these losses, essential ecosystem functions on which civilization depends are deteriorating

(Cardoso et al. 2020). Because insects rely on environmental temperature to regulate their physiological functions, continuous exposure to maximum temperatures makes it extremely difficult for them to survive. As a result, an atmosphere with a rising temperature due to global warming will be unsuitable for insect life (González Tokman et al. 2020). Many species' distributions and abundances are expected to shift due to climate change, affecting other species in the newly exposed region (Mclaughlin et al. 2002). With global warming, significant changes in insect diversity, regional distribution of insect pests, and insect population dynamics are projected (Sharma et al. 2014) (Karuppaiah et al. 2012). Increased temperature, changing precipitation patterns, and rising CO2 levels impact insects, greatly expanding their range and causing epizootics (Raza et al. 2015). Geographic range losses caused by climate change resulting in a 3.2ºC increase in temperature may result in a loss of more than 50% of the geographic range of 49 percent of insects (Warren et al. 2018).

Based on predictions from various scientists, an increase of 0.5ºC to 4ºC is expected in various parts of India. Silkworm, *B. mori* being a poikilothermic insect and being so sensitive to the ambient temperature for its growth and development, is directly affected by environmental factors especially, temperature. Sericulture in India is practiced mainly in tropical belts such as Karnataka, Andhra Pradesh, Tamil Naidu, and West Bengal, and bivoltine sericulture practiced in the temperate belt like Jammu and Kashmir and Uttrakhand, will then get a hit due to climate change and rise in temperature, thus incurring a huge loss on the economic sector related to sericulture of those areas (Ram et al. 2016). Silkworm *B. mori* of multivoltine breed cultivated in the tropics are naturally more thermotolerant than bivoltines. A permanent rise in temperature of a few degrees, however, will be outside of their tolerance range as heat shock proteins which normally come into play as the worm encounters heat shock, can't however work if the temperature is above the tolerance range for a more extended period. Effects of increased temperature on silkworm biology as well as yield can be incurred. A decrease in the yield of cocoon crops and sometimes failure of a crop due to disease has been noticed in *B. mori* due to global warming and abnormal rainfall patterns (Sharma et al. 2020). A temperature rise shortens the immature development of *B. mori* (M2P2 variety) (Islam, 2018). Larval mortality in silkworm breed (CSR2 x CSR4) increased with an increase in temperature, and the best growth was at 22ºC to 24ºC with a relative humidity of 80-85% (Verma et al. 2011). It is clear from the literature that *B. mori* gets negatively affected by a rise in temperature. Based on this and research about silkworm thermotolerance, we predict that a harsh impact on silkworm biology and crop production from sericulture will be felt due to temperature rise by global warming in the coming decades.

An increase in temperature can also have a disastrous effect on non-mulberry sericulture, like the muga silk industry and muga silkworm *Antheraea assamensis*. Annually giving six crops out of which two are commercial, muga silk farming needs optimum temperature for productivity. An increase in temperature or change in humidity status can be detrimental to this industry. A study conducted provides evidence that is in line with the fears mentioned above. In the survey, cocoon yield, moth emergence, hatching percentage m fecundity, and cocoon yield were studied, and it was observed that in the year 2008, cocoon yield was 45/dfl as compared to 76/dfl in 1995. Also, moth emergence was highest in 1995 compared to 2000, which experienced the highest temperature variation. On total fecundity, hatching percentage, moth emergence, and cocoon yield were decreased compared to previous years, all of this due to a rise in slight temperature (Zamal et al. 2010).

Biomarkers for thermotolerance in *B. mori* and their prospect concerning global warming

ISSR & SSR MARKERS: Some silkworm races are tested for their tolerance to thermal stress using quantitative traits, while the heat shock response in *B. mori* has previously been examined through the induction of heat shock proteins. Kumar et al. (2001) and Koundinya et al. 2003 reported that any *B. mori* race or breed showing a pupation rate above 80% at 36ºC might be considered as thermo-tolerant. Nowadays, new molecular techniques like the use of PCR-based DNA markers are used to screen *B. mori* for thermotolerance. Using molecular markers like ISSR (Inter Simple Sequence Repeats) for identification of thermotolerant silkworm breeds during breeding programs provides a viable option for screening thermotolerant varieties, as demonstrated in an experiment in which 15 silkworm races were tested for thermotolerance and pupation rates. In a lab setting, the thermal stress of 36ºC for six h a day daily until spinning was given and was used as an indicator of thermotolerance. Six breeds (A4e (86%), MH-MP(Y) (84.5%), CB5 (84%), race O (83%), race B (82%), and Kolar Gold (81%) were selected as thermotolerant on the basis of pupation rate (=81%). Subsequent DNA extraction and PCR- ISSR analysis on all 15 races revealed that a total of five bands showing a correlation with pupation rate after thermal stress and was in line with the above thermotolerant races detected from pupation rates. With the backing of strong statistical analysis of the data generated, it was confirmed that these 5 ISSR markers could be used as markers for thermotolerance and thus can help in breeding programs for the development of thermotolerant breeds (Shrivastava et al. 2007).

Chandrakanth et al. (2015) used marker-assisted selection and identified SSR (Simple Sequence Repeats) sequences to screen thermotolerant breeds. With the help of bulk segregation analysis (BSA), which reduces many markers to a few specific and highly linked to the trait, researchers identified and narrowed down target marker SO816, which can be used for screening during the breeding process for selection of thermotolerant bivoltine breeds. In another study, under lab setting on V^th^ instar larvae, two microsatellite primer pairs viz., S0803 and S0816 were reported to be linked to thermotolerance in silkworm and were used to screen thermotolerant breeds. Thermotolerant and thermos-susceptible breeds were successfully screened via amplification of these two molecular markers. The study concluded that silkworm breeds like B.Con-1, B.Con-4, SK6, and SK7 are tolerant to high temperatures (Chandrakanth et al. 2018). Thus, taking advantage of these techniques, we can identify thermotolerant silkworm breeds and use them as parents during breeding programs to develop new thermotolerant breeds that are expected to be more thermotolerant than their parents as was shown by Kumar et al. (2001).

Esterases and catalase: Esterases are found in the whole of living organisms ubiquitously and play a slew of roles in plants, animals, and microorganisms. In insects, it has a significant role in defense. The part of esterase has been found in toxic detoxifying materials in various breeds like Nistari*,* Kollegal Jawan, and Hosa Mysore. Thus, it can be used as a biomarker for determining genetic hardiness in response to toxic materials (Priya & Somasundaram, 2019). The role of esterase in the thermotolerance of silkworm has been studied. Two *B. mori* breeds Hoya mysori and Ap12 have been studied for the role of esterases in providing hardiness to these breeds (Vishnupriya & Somasundaram, 2012). The presence of esterases in haemolymph of *B. mori* has also been detected and their role in thermotolerance of both multivoltine and bivoltine races studied. An experiment conducted in lab setting showed the tolerance of esterase from silkworm to temperatures of 70ºC for 10 minutes, therefore, indicating their possible role in the thermotolerance of *B. mori* (Patnik et al. 2012). Genomic organization of blood esterase gene of silkworm races (pure Mysore, PMX, NB4D2, and CSR 19) indicated the presence of two exons of 192 bp and 524 bp and a long intron of 2124 bp (Ponnuvel et al. 2008). When exposed to five different temperature regimes viz. 25 ± 1ºC, 32 ± 1ºC, 34 ± 1ºC, 36 ± 1ºC and 38 ± 1ºC for 6h per day, breeds Nistari and Cambodge, D6(P) and SK4, D6(P)N and SK4C (near isogenic lines) and identification of heat stable esterase done by incubating the electrophoresed acrylamide gel containing haemolymph to 60ºC for 15 minutes. The experiment was successful in identifying five different isoforms of alpha esterase. Esterase 2 and esterase 3 as heat stable (Moorthy et al. 2016). In selected tropical silkworm breeds (CB5 and its syngenial lines CB5Lme-1, CB5Lm-2, and CB5Lm-5), esterase isozyme polymorphism has been found in esterases in haemolymph and digestive juice (Chattopadhyay et al. 2001). Two heat-stable esterases were found in both multivoltine and bivoltine selected breeds and their near-isogenic lines (Moorthy et al. 2016). Apart from these biomarkers, catalase biomarker has also been found to have a positive correlation with thermotolerance of silkworm breeds JROP, KA, and NB4D2 breeds (Nabizadeh et al. 2011).

The use of these biomarkers, whether enzymatic or molecular, will prove handy during the screening of thermotolerant varieties of *B. mori*. These screening methods if done on a large scale and supported by strong government policies can serve as a prelude for the distribution of more thermotolerant varieties to farmers. This will, in turn, make the silk industry well prepared for the coming global warming effects, i.e., rise of a few degrees in temperature. Although global warming and a permanent rise in temperature will be harmful for the silk industry, steps taken now to prepare and counter the expected should be encouraged.

Global warming effects on other organisms

By extending the geographic range of currently harmful species and selecting for adaptive thermotolerance in species with high pathogenic potential that are currently non-pathogenic due to mammalian temperatures, global warming will cause novel fungal infections in mammals (Garcia-Solache et al. 2010). Increased temperatures will have an impact on interactions between heterotrophs and autotrophs (such as pollination and seed dispersal) as well as between heterotrophs (such as predators-prey, parasites/pathogens-hosts). These interactions will generally have a negative impact on essential ecosystem services (tasks that directly benefit human society, like pollination), and there is a possibility that species co-extinction rates will increase (Traill et al. 2010). Although it is frequently noted that temperature tolerance phenotypic plasticity (thermal acclimation) is a crucial aspect of acute and evolutionary adaptation to temperatures in insects, in some insect species, such as Drosophila, the plasticity of upper thermal limits is small in magnitude, evolves slowly, and acclimation ability is weakly correlated with latitude and environmental heterogeneity. As a result, upper thermal limit plasticity is unlikely to adequately buffer the consequences of global warming for species that are already close to their upper thermal limits (Sørensen et al. 2016). Climate change is also shifting the gene arrangement frequencies in *Drosophila subobscura*. In Europe and South and North America, but it remains unclear why (Rezende et al. 2010).

Mass deaths of Mediterranean benthic marine invertebrates were recorded in places with positive temperature trends with cnidarians and sponges being most affected. Western Mediterranean mass deaths are most common. The two most dramatic episodes (1,000 km of coastline and 30 macro-benthic species, including sponges, cnidarians, bivalves, ascidians, and bryozoans) occurred in the north-western Mediterranean coasts in 1999 and 2003. These two episodes coincided with 3-4ºC above-average temperatures and late summer water column stability (Rivetti et al. 2014). Both rising ocean temperatures and greater CO_2 levels appear to be harmful to coral reef fish. Despite variances in heat sensitivity among species, the majority of species studied so far appear to dwell near their thermal optimum. Even slight increases in average temperature reduce aerobic scope, causing growth, reproductive output, swimming ability, and, in certain circumstances, survival to suffer (Munday et al. 2012). In aquatic environments, phytoplankton is the primary source of energy and omega-3 (n-3) long-chain essential fatty acids (EFA). Their growth and biochemical makeup are influenced by their surroundings, particularly temperature, which continues to rise as a result of climate change. The temperature was found to be closely linked to a decrease in n-3 long-chain polyunsaturated fatty acids (LC-PUFA) and an increase in omega-6 and saturated fatty acids. As a result of reduced production of these EFA as a result of climate change, animals that rely on these chemicals for optimal physiological function are expected to suffer (Hixson et al. 2016).

In recent decades, animal populations have experienced significant decreases. These decreases have happened in the context of rapid, human-caused environmental change, such as climate change. We discovered that losses in avian and mammalian population abundance are greater in locations where the mean temperature has grown more rapidly and that this effect is more pronounced for birds (Spooner et al. 2018).

Conclusion

Bivoltine *B. mori* generates higher-quality silk but are more susceptible to severe temperatures than multivoltine *B. mori*, which produce lower-quality silk. Changes in thermotolerance are caused by differences in the expression of heat shock genes and proteins in bivoltine and multivoltine *B. mori*. *B. mori* responds to heat shock by boosting the expression of heat shock proteins. Different organs express different heat shock proteins differently and of different types. Heat shock proteins protect the body of silkworm from the insults of heat shock but only up to a certain limit above which their protective effect fails. A rise in temperature above the optimal growing temperature of silkworm affects the life cycle as well as the economic characters of *B. mori*. Owing to the global increase in temperature of ~1.5ºC to = 2ºC in the coming decades and up to 5ºC at the start of the next century, may wreak havoc on the silk industry generally practiced by marginalized and economically weaker sections of society. The negative consequences will be much more pronounced in bivoltine *B. mori*, as they are exclusively adapted to a temperate climate and even a small increase in temperature can be harmful. Therefore, the future challenge of global warming warrants measures to increase the thermotolerance of *B. mori*. Some bivoltine worms are more thermotolerant than their other counterparts, increased commercialized culture of these worms on large scale and more inter-breeding between the thermotolerant breeds should be preferred. Taking advantage of molecular markers like ISSR and SSR markers and enzymatic markers like esterases and catalases, thermotolerant varieties should be screened and bred. Research should also focus on searching for new molecular markers in the silkworm genome associated with thermotolerance, which may help in the easy screening of thermotolerant breeds. These suggested methods might come in handy when devising the policies of silkworm breeding and advising farmers which in turn can thwart the potential ill effects of a rise in temperature due to global warming. Although with global warming, *B. mori* will not be the only organism that will get affected. Other organisms will also get affected, mostly in a negative way. However, here in this article, we focused mainly on the *B. mori* in this regard. Therefore, the predictions on harmful effects of temperature rise on *B. mori* should not be generalized to other organisms.

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