



唐思琼, 梁馨元, 苏杰, 张建萍. 螨类耐寒性及其机理研究进展 [J]. 环境昆虫学报, 2023, 45 (4): 871–880.

## 螨类耐寒性及其机理研究进展

唐思琼, 梁馨元, 苏杰, 张建萍\*

(石河子大学农学院, 新疆绿洲农业病虫害治理与植保资源利用重点实验室, 新疆石河子 832000)

**摘要:** 耐寒性的高低极大程度上影响螨类的越冬存活以及分布扩散情况。螨类耐寒性评估的主要指标是过冷却点以及低温胁迫下的致死温度和致死时间。螨类耐寒性通常具有可塑性, 不同发育时期、滞育、季节变化以及冷驯化均会影响耐寒性, 而耐寒性的变化涉及复杂的分子水平以及生理生化物质的变化。本文简要介绍了目前评估螨类耐寒性的生物学指标以及影响螨类的耐寒性的因素, 总结了螨类耐寒性变化所涉及的生理生化和分子机制, 探讨了目前螨类耐寒性需要进一步研究的科学问题, 并对螨类耐寒性研究的生态学意义进行了展望。以期对螨类耐寒性的深入研究提供参考, 促进害螨的综合防治和天敌捕食螨的开发利用。

**关键词:** 低温耐受性; 过冷却点; 冷驯化; 低温保护物质

中图分类号: Q968.1; S433

文献标识码: A

文章编号: 1674-0858 (2023) 04-0871-10

### Research progress on mite cold tolerance and its mechanism

TANG Si-Qiong, LIANG Xin-Qi, SU Jie, ZHANG Jian-Ping\* (Key Laboratory of Oasis Agricultural Pest Management and Plant Protection Resources Utilization, Xinjiang Uygur Autonomous Region, College of Agriculture, Shihezi University, Shihezi 832000, Xinjiang Uygur Autonomous Region, China)

**Abstract:** Cold tolerance greatly influences the overwintering survival and distribution of mites. The major indicators of cold tolerance for mites are the supercooling point and lethal temperature and time under low temperature. Cold tolerance of mite is plastic, which is affected by developmental stage, diapause, seasonal changes, and cold acclimation. However, the change of cold tolerance involves the complex changes of molecular level and the physiology-biochemical substance. Firstly, this paper briefly introduces the biological indicators for evaluating the cold tolerance of mites and the factors affecting the cold tolerance of mites. Then, it summarizes the physiological, biochemical, and molecular mechanisms relate to the change of mite's cold tolerance. Furthermore, the problems that need to be further studied were discussed, and the ecological significance of the study on mite cold tolerance was prospected. It is expected to provide the reference for the deep study of mite cold tolerance, thus promoting the integrated control of harmful mites and the utilization of predatory mites.

**Key words:** Cold tolerance; supercooling point; cold acclimation; cryoprotective compounds

在节肢动物中, 螨类数量多, 物种丰富, 分布广泛, 于温带、热带、亚热带、甚至极地等地区均有分布 (Luypaert *et al.*, 2015; Amani *et al.*, 2020; Brunetti *et al.*, 2021)。温度是影响螨类生长

基金项目: 国家自然科学基金 (32060635); 国家重点研发计划 (2017YFD0201900); 兵团区域创新引导计划 (2018BB043); 石河子大学青年创新人才计划 (CXPY202002); 石河子大学自主资助支持校级科研项目 (ZZZC202114)

作者简介: 唐思琼, 女, 1996年生, 新疆人, 博士, 研究方向为植物保护, E-mail: 1595018219@qq.com

\* 通讯作者 Author for correspondence: 张建萍, 女, 博士, 教授, 研究方向为植物保护, E-mail: zhjp\_agr@shzu.edu.cn

收稿日期 Received: 2022-04-28; 接受日期 Accepted: 2022-08-02

发育、繁衍生存、分布范围的重要因素,尤其是在温带和寒带地区,冬季低温条件是螨类生存的巨大挑战。螨类本身具有一定的抗冻耐寒能力,并且可以感知环境温度,通过一系列行为和生理对策(滞育、温度适应)提高耐寒性,应对环境压力(Ghazy *et al.*, 2016)。通常根据螨类抗寒性的生理生化机制的不同将螨类分为两种类型:结冰耐受型(Freeze tolerant)和避免结冰型(Freeze avoiding);结冰耐受型的螨类能忍受细胞外体液结冰而不死亡;避免结冰型的螨类,通过增强过冷却能力,使自身的结冰温度降低,温带和寒带的螨类多为该类型(Sinclair *et al.*, 2015; Andreadis and Athanassiou, 2017)。螨类的耐寒性是可塑的,并受到多种因素的影响,如温度变化、季节更替、地理差异、食物营养、发育阶段等(Worland and LukesřlovaÅ, 2000; Hawes *et al.*, 2007b; Izadi *et al.*, 2019; Keosentse *et al.*, 2021)。耐寒性的研究对于揭示螨类的物种分布、种群波动、综合控制和天敌的开发利用等具有重要意义。本文从螨类的耐寒性生物学特性、耐寒性影响因素和耐寒性机理这3个方面进行总结,以期对螨类耐寒性的研究提供参考。

## 1 螨类耐寒性评估生物学指标

### 1.1 过冷却点

大多数昆虫和螨类中都存在一种过冷却现象,即环境温度低于其体液冰点时,体液仍能保持液体状态的现象(秦明等, 2017; Masoumi *et al.*, 2021)。过冷却点则是指螨类和昆虫体液开始结冰时的温度(White *et al.*, 2018; Bleiker and Smith, 2019)。过冷却点是螨类及昆虫耐寒性研究的重要指标,不同螨类的过冷却能力不尽相同,受生理状态、体型大小、生活史阶段和季节等因素的影响(Ghazy *et al.*, 2016; 史彩华等, 2016)。目前螨类过冷却点测定的原理是:将螨类放置于逐渐降温的环境中,当螨类体液开始结冰,螨体会放热现象,放热升温,螨体温度回升,温度开始上升的起点即为过冷却点。

目前螨类过冷却点测定方法根据所用仪器不同分为两种。一是使用热电偶。将螨体固定在热电偶上,热电偶可以测量螨体的温度,然后放入冰箱或者降温仪器中,以一定的速率逐渐降温,热电偶另一端与计算机相连记录螨体的温度变化

(Broufas and Koveos, 2001a)。二是使用差示扫描量热仪(Differential scanning calorimeter, DSC)(Hart *et al.*, 2002; Hatherly *et al.*, 2004),将螨放置于DSC专用的铝皿中,封闭铝皿,放入DSC中,DSC以一定的速率逐渐降温,与DSC连接的计算机软件会记录铝皿内的温度变化。

### 1.2 致死温度和致死时间

除了过冷却点的检测,另一个螨类耐寒性生物学评估指标是螨类在低温下的存活状态,通常将螨类置于不同温度梯度下一定时间,或者置于某一温度不同时间下,恢复正常温度,24 h后检测螨类的死亡率或者存活率,使用Probit模型分析螨类致死温度(Lower lethal temperature)和致死时间(Lower lethal time)(Khodayari *et al.*, 2012; Luypaert *et al.*, 2015),致死温度和致死时间的检测更加明确了低温对螨类种群的胁迫作用,可预测螨类在低温下的存活情况。

## 2 螨类耐寒性影响因素

### 2.1 发育阶段

处于不同发育阶段的螨类,耐寒性有所差异。对螨类过冷却点的检测发现,大多数螨类的卵或者幼螨的过冷却点低于成螨(表1),例如智利小植绥螨 *Phytoseiulus persimilis* (Athias-Henriot, 1957),胡瓜新小绥螨 *Neoseiulus cucumeris* (Oudemans, 1930)和巨毛植绥螨 *Phytoseiulus macropilis* (Banks, 1904),推测原因是卵或者幼螨尚未取食,体内冰核物质较少(Morewood, 1992; Coombs and Bale, 2014)。然而,高山小盲绥螨 *Typhlodromips montdorensis* (Schicha, 1979)成螨和幼螨的过冷却点没有明显差异(Hatherly *et al.*, 2004)。过冷却点并不是耐寒性高低评价的唯一标准,即使幼螨的过冷却点低于成螨,但在低温胁迫试验中发现,成螨在低温下的存活能力普遍高于幼螨(Ghazy *et al.*, 2012; Ito and Chae, 2019)。

此外,在南极阿拉斯加甲螨 *Alaskozetes antarcticus* (Michael, 1903)发现了一种有趣的现象,无论环境温度如何变化,野外采集和经过冷驯化(5℃)后的成螨在蜕皮状态下都具有较低的过冷却点(Hawes *et al.*, 2007a)。在弹尾目昆虫中发现了同样的现象,推测可能是因为弹尾目昆虫通过蜕皮蜕掉了体内冰核物质(Worland *et al.*,

2006; 史彩华等, 2016), 但在螨类中尚未研究报道原因。

## 2.2 滞育

滞育是节肢动物应对不利环境的一种普遍对策 (姜春艳等, 2021)。滞育在螨类越冬中发挥重要作用, 显著影响螨类对低温的耐受能力 (Bryon *et al.*, 2017)。例如, 二斑叶螨 *Tetranychus urticae*

(Koch, 1836) 雌成螨进入滞育后, 过冷却点显著降低, 低温致死率降低 (Khodayari *et al.*, 2012; Khodayari *et al.*, 2013b; White *et al.*, 2018)。芬兰真绥螨 *Euseius finlandicus* (Oudemans, 1915) 滞育雌成螨于  $-12^{\circ}\text{C}$  暴露 2 h 后全部死亡, 而非滞育雌成螨置于  $-11^{\circ}\text{C}$  则全部死亡 (Broufas and Koveos, 2001b)。

表 1 不同发育阶段螨类的过冷却点

Table 1 Supercooling point of mite at different developmental stages

物种 Species	过冷却点 ( $^{\circ}\text{C}$ ) Supercooling point							参考文献 References
	卵 Egg	幼螨 Larve	若 I Protonymph	若 II Deutonymph	雌成螨 Female adult		雄成螨 Male adult	
					非滞育 Non-diapause	滞育 Diapause		
芬兰真绥螨 <i>Euseius finlandicus</i>	$-27.6 \pm 0.41$	$-24.0 \pm 0.37$	$-21.7 \pm 0.36$	$-22.9 \pm 0.33$	$-22.8 \pm 0.47$	$-23.1 \pm 0.70$	$-21.9 \pm 0.56$	Broufas and Koveos, 2001a
智利小植绥螨 <i>Phytoseiulus persimilis</i>	$-25.0 \pm 1.22$	$-25.0 \pm 1.41$	$-24.2 \pm 1.09$	$-23.9 \pm 0.71$	$-22.5 \pm 0.90$	-	-	Morewood, 1992
胡瓜新小绥螨 <i>Neoseiulus cucumeris</i>	$-27.1 \pm 1.23$	$-25.7 \pm 1.73$	$-22.0 \pm 2.43$	$-19.4 \pm 1.96$	$-20.7 \pm 0.77$	$-21.6 \pm 1.40$	$-21.9 \pm 1.63$	
二斑叶螨 <i>Tetranychus urticae</i>	-	-	-	$-25.3 \pm 0.30$	$-19.1 \pm 0.50$	$-22.6 \pm 0.30$	$-21.3 \pm 0.50$	White <i>et al.</i> , 2018
温氏新小绥螨 <i>Neoseiulus womersleyi</i>	-	-	-	-	$-22.9 \pm 0.23$	$-23.3 \pm 0.39$	-	Gotoh <i>et al.</i> , 2005
腐食酪螨 <i>Tyrophagus putrescentiae</i>	$-35.6 \pm 0.40$	-	-	$-26.5 \pm 0.40$	$-24.2 \pm 0.50$	-	-	Eaton and Kells, 2011
巨毛植绥螨 <i>Phytoseiulus macropilis</i>	-	$-23.3 \pm 0.20$	-	-	$-21.7 \pm 0.30$	-	-	Coombs and Bale, 2014
高山小盲绥螨 <i>Typhlodromips montdorensis</i>	-	$-24.3 \pm 0.38$	-	-	$-24.1 \pm 0.61$	-	-	Hatherly <i>et al.</i> , 2004

注 “-” 指该螨的过冷却点未知, 下表同。Note “-” indicated the supercooling point of mite was unknow. The same as below.

## 2.3 季节

季节变迁是影响螨类耐寒能力的因素之一。秋季, 气温逐渐降低诱导节肢动物产生一系列生理适应过程提高它们的耐寒性 (Jensen *et al.*, 2019)。大量研究表明, 螨类的耐寒性存在明显的季节分化, 通常越冬种群过冷却点降低, 可承受

更低的温度的胁迫 (表 2) (Sjursen and Sømme, 2000; Khodayari *et al.*, 2013a; Ghazy *et al.*, 2016)。梨盲走螨 *Typhlodromus pyri* (Scheuten, 1857) 的过冷点显著受到季节的影响, 在 7-9 月过冷却点为  $-18.2^{\circ}\text{C}$ , 10 月为  $-23.2^{\circ}\text{C}$ , 在较冷的 11 月至 3 月其过冷却点下降至  $-28.2^{\circ}\text{C}$

(Moreau *et al.*, 2000)。蚁食菌螨 *Anoetus myrmicarum* (Scheucher, 1957) 成螨冬季的过冷却点低于夏季, 相差 17°C 以上 (Zhigulskaya and

Berman, 2014)。南极阿拉斯加甲螨的耐寒性表现出明显的季节变化规律, 低过冷却点个体的比例随着温度的降低而增加 (Hawes *et al.*, 2007a)。

表 2 不同季节下螨类过冷却点

Table 2 Supercooling point of mite one the different season

物种 Species	季节 Season	过冷却点 (°C) Supercooling point	参考文献 References
梨盲走螨 <i>Typhlodromus pyri</i>	夏季 (1995. 07) Summer	-17.75 ± 0.91	Moreau <i>et al.</i> , 2000
	冬季 (1995. 11) Winter	-28.06 ± 0.83	
蚁食菌螨 <i>Anoetus myrmicarum</i>	夏季 Summer	-7.1 ± 0.2	Zhigulskaya and Berman, 2014
	冬季 Winter	-25.8 ~ -27.7	
二斑叶螨 <i>Tetranychus urticae</i>	春季 (2011. 04) Spring	-20.8 ± 3.3 (中值)	Khodayari <i>et al.</i> , 2013a
	冬季 (2010. 11) Winter	-23.5 ± 2.3 (中值)	
异绒螨 <i>Allothrombium</i> sp.	春季 (2017. 05) Spring	-6.9	Anthony and Sinclair, 2019
	冬季 (2017. 01) Winter	-8.4	
	春季 (2014. 04 ~ 05) Spring	-17.9	
麦岩螨 <i>Petrobia latens</i>	夏季 (2014. 06) Summer	-17.3	Sitz <i>et al.</i> , 2019
	秋季 (2014. 10) Autumn	-16.4	
	冬季 (2014. 02, 12, 2015. 01) Winter	-16.7	
单奥甲螨属 <i>Phauloppia</i> sp.	夏季 (1998. 07) Summer	-9.4 ± 2.3	Sjursen and Sømme, 2000
	冬季 (1998. 01) Winter	-35.3 ± 5.8	

## 2.4 冷驯化

昆虫在经历低温锻炼后, 其抵抗低温伤害的能力增强的现象称为冷驯化 (唐斌等, 2014)。根据冷驯化时间长短可将其分为两种类型, 一是长时间驯化, 即昆虫通过几天甚至几周的低温锻炼, 从而获得抗低温能力; 另一种是短时间驯化, 也称快速冷耐受 (Rapid cold hardening, RCH), 即昆虫在低温下经历几个小时甚至几十分钟的锻炼, 从而耐寒性提高 (岳雷等, 2013; 沈祖乐等, 2017; 张小香等, 2021)。长时间驯化和快速冷耐受在螨类耐寒性研究中均有涉及, 多关注于冷驯化对过冷却点和低温存活能力的影响。冷驯化的温度和时间因螨种类而有所差异, 通常螨类冷驯化温度在 0 ~ 15°C (Morewood, 1992; Deere *et al.*, 2006; Khodayari *et al.*, 2012; Jensen *et al.*, 2017)。不同螨类对于冷驯化的生理响应机制不同, 耐寒能力提升程度不同。但多数螨类经过冷驯化后或多或少其耐寒性有所提高。加州新小绥螨 *Neoseiulus californicus* (McGregor, 1954) 在 5°C 驯化 1 h 后再

置于 -10°C 暴露 2 h, 存活率相比对照提高了 70% 以上 (Ghazy and Amano, 2014)。芬兰钝绥螨 *Euseius finlandicus* Oudemans 雌成螨于 5°C 驯化 1 ~ 2 周后, 过冷却点无明显变化, 但在 -15°C 的低温下其存活时间有所延长 (Broufas and Koveos, 2001a, 2001b)。高山小盲绥螨成螨和幼螨于 10°C 驯化 7 d 后, 过冷却点虽没有明显的变化, 但是相比于未驯化的雌成螨, 驯化后的雌成螨可以耐受更低的温度 (Hatherly *et al.*, 2004)。二斑叶螨雌成螨和雄成螨同样在 10°C 驯化 7 d 后, 过冷却点显著降低 (White *et al.*, 2018) (表 3)。

## 2.5 其它因素

螨类耐寒性的可塑性还表现在对不同气候条件的适应方面。不同的地理位置引起的气候条件的差异也间接影响螨类耐热性和耐寒性的变化, 赤足地螨 *Halotydeus destructor* (Tucker, 1925) 原是南非本地种, 后入侵澳大利亚逐渐适应当地的气候, 成为澳大利亚主要的农业害虫, 研究发现澳大利亚赤足叶螨种群与南非种群的耐寒性有所

表 3 冷驯化对螨类过冷却点的影响  
Table 3 The effect of cold acclimation on supercooling point of mite

种类 Species	驯化温度 (°C) Acclimation temperature	驯化时间 (d) Acclimation time	过冷却点 (°C) Supercooling point		参考文献 References
			未驯化 Non-acclimation	驯化 acclimation	
马里恩海甲螨 <i>Halozetes marionensis</i>	0	7	-	-20.3 ± 0.9	Deere <i>et al.</i> , 2006
	5	7	-	-12.8 ± 1.3	
	10	7	-	-9.0 ± 1.4	
	15	7	-	-5.0 ± 0.7	
金黄海甲螨 <i>Halozetes fulvus</i>	0	7	-	-16.3 ± 1.1	Hatherly <i>et al.</i> , 2004
	5	7	-	-18.5 ± 1.2	
	10	7	-	-15.8 ± 0.6	
高山小盲绥螨 <i>Typhlodromips montdorensis</i>	10	7	-24.1 ± 0.61	-22.4 ± 0.48	Morewood, 1992
	7.5	7	-22.5 ± 0.90	-22.4 ± 0.84	
	7.5	7	-20.7 ± 0.77	-22.1 ± 1.0	
智利小植绥螨 <i>Phytoseiulus persimilis</i>	10	7	-19.1 ± 0.5	-22.0 ± 0.6	White <i>et al.</i> , 2018
	0	10	-19.6 ± 0.5	-21.4	
	5	10	-19.6 ± 0.5	-22.2	
胡瓜新小绥螨 <i>Neoseiulus cucumeris</i>	10	7	-19.1 ± 0.5	-22.0 ± 0.6	Khodayari <i>et al.</i> , 2012
	0	10	-19.6 ± 0.5	-21.4	
比利时海甲螨 <i>Halozetes belgicae</i>	10	7	-7.6	-19.4 (中值)	Hawes <i>et al.</i> , 2007b

差异,甚至在澳大利亚不同气候地区的种群之间的耐寒性也有所变化 (Hill *et al.*, 2013)。食物对螨类耐寒性也具有一定影响,南极阿拉斯加甲螨取食含有冰核的藻类 *Prasiola crispa* (Lightfoot, 1837) 后,有耐寒性降低的现象 (Worland and LukesĽovaĽ, 2000)。加州新小绥螨在低温 (7.5°C) 贮藏前饲喂富含低温保护剂、抗氧化物质以及能量物质的滞育二斑叶螨可以提高加州新小绥螨的贮藏效果,间接反映了食物对该捕食螨低温耐受型提升的重要性 (Ghazy *et al.*, 2013)。

### 3 螨类耐寒性的生理生化和分子机制

螨类越冬存活或者耐寒性的提高,取决于体内的生理调节,特别是与滞育和冷驯化相关的调

控机制,包括抗冻保护物质、能量储备物质的积累和新陈代谢的改变,这些调节对于螨类耐寒性的提高具有重要作用 (Morewood, 1992) (表 4)。

#### 3.1 抗冻保护物质和能量物质的积累

昆虫和螨类抗冻耐寒的关键生理机制之一是一些小分子量低温保护物质 (Low molecular mass cryoprotective compounds, CPs) 的积累,其种类和数量因物种而异,诸如甘油、葡萄糖、海藻糖、果糖等 (陈豪等, 2010; Teets and Denlinger, 2014; Des Marteaux *et al.*, 2019)。甘油是昆虫和螨类中最常见的低温保护物质,螨类的耐寒性与甘油的含量密切相关。已有研究发现甘油是南极阿拉斯加甲螨和拉氏革塞螨 *Gamasellus racovitzai* (Trouessart, 1903) 成螨和若螨中存在的主要低温保护物质,表现出明显的季节波动并在在冬季积累量显著增加。异绒螨成螨在寒冷的冬季,血淋

巴渗透压和甘油浓度升高,含水量降低。Riddick and Wu (2010) 研究发现为贮藏期的智利小植绥螨提供低温保护剂物质如甘油、乙二醇或者碳水化合物葡萄糖、蔗糖等一定程度上可以增加捕食螨在低温下的存活率,促进贮藏效果,间接体现了低温保护物质对低温下捕食螨的保护作用。

### 3.2 激活保护酶活性

在恶劣的环境下,例如低温,极易诱导昆虫或螨类细胞代谢的变化导致活性氧 (Reactive oxygen species, ROS) 的积累,引发生物细胞的严重损伤。昆虫在低温胁迫下为避免氧化应激,通常采用两种策略,一是增加抗氧化酶活性 (避免结冰型昆虫),二是降低代谢从而减少活性氧的产生 (结冰耐受型昆虫) (Lubawy *et al.*, 2022)。在

螨类抗氧化能力研究中发现,低温胁迫下螨类的抗氧化机制激活,通过增加抗氧化酶的活性,清除细胞内的活性氧、羟自由基及其他过氧化物,降低对细胞的损伤。例如腐食酪螨 *Tyrophagus putrescentiae* 和柑橘全爪螨 *Panonychus citri* (McGregor, 1916) 在低温下 (0, 5, 10, 15°C) 超氧化物歧化酶 (Superoxide dismutase, SOD) 和谷胱甘肽-S-转移酶 (Glutathione-S-transferase, GST) 活性增强; 胡瓜新小绥螨在低温暴露下 SOD 和过氧化物酶 (Peroxidase, POX) 活性增强 (Zhang *et al.*, 2014; 杨丽红等, 2016; 王静等, 2019)。低温胁迫下抗氧化酶活性增强可能是螨类耐寒性增强的原因之一。

表 4 低温胁迫后或越冬螨类低温保护物质以及相关基因的变化

Table 4 Changes in cryoprotective compounds and related genes of mites after cold stress or during the winter

物质/基因 Compounds/ Gene	物种 Species	参考文献 References
小分子低温保护物质 Low molecular mass cryoprotective compounds	甘油 Glycerol ↑ (冬季 winter)	南极阿拉斯加甲螨 <i>Alaskozetes antarcticus</i> 拉氏革塞螨 <i>Gamasellus racovitzai</i> 异绒螨 <i>Allothrombium</i> sp.
酶 Enzyme	SOD ↑ (冷胁迫 cold stress)	腐食酪螨 <i>Tyrophagus putrescentiae</i> 柑橘全爪螨 <i>Panonychus citri</i> 胡瓜新小绥螨 <i>Neoseiulus cucumeris</i>
	GST ↑ (冷胁迫 cold stress)	腐食酪螨 <i>Tyrophagus putrescentiae</i> 柑橘全爪螨 <i>Panonychus citri</i>
	POX ↑ (冷胁迫 cold stress)	胡瓜新小绥螨 <i>Neoseiulus cucumeris</i>
蛋白质 Protein	<i>Hsp90</i> ↑ (冷胁迫 cold stress)	朱砂叶螨 <i>Tetranychus cinnabarinus</i>
	<i>Hsp90</i> ↑ <i>Hsp70</i> ↑ (冷胁迫 cold stress)	胡瓜新小绥螨 <i>Neoseiulus cucumeris</i>

注 “↑”表示表达量 (活性) 上升。Noté “↑” meant the level (activity) was increased.

### 3.3 积累大分子蛋白质

昆虫和螨类的耐寒性与多种蛋白质密切相关。近年来,在多种生物体内发现了与耐寒性相关的蛋白质,如热激蛋白 (Heat shock proteins, *Hsps*), 抗冻蛋白 (Antifreeze Proteins, *Afps*), 水通道蛋白 (Aquaporins, *Aqps*) 等 (Enriquez and Colinet, 2019; Teets *et al.*, 2019)。

抗冻蛋白是一类吸附在冰核表面,降低体液冰点和过冷却点,抑制冰核增长的冰结合蛋白,具有热滞活性可成为热滞蛋白 (Clark and Worland, 2008)。大多数产生抗冻蛋白的节肢动物为避免结冰型 (Duman *et al.*, 2004)。Block and Duman (1989) 在南极阿拉斯加甲螨中发现了抗冻蛋白 (Block and Duman, 1989)。此后, Sjørnsen

and Sømme 在单奥甲螨属 *Phauloppia* sp. 成螨中发现了明显的热滞现象, 验证了热滞蛋白的存在 (Sjursen and Sømme, 2000)。Bryon *et al.* (2013) 在滞育的二斑叶螨中发现了类似抗冻蛋白的基因, 且滞育会诱导该基因上调表达。但螨类抗冻蛋白的相关研究较少, 该蛋白对于螨类耐寒性的调控机制尚不明确。

热激蛋白是一类抗逆蛋白, 多在环境胁迫下应激表达, 具有保护细胞不受伤害的作用 (史彩华等, 2016)。多项研究发现热激蛋白基因与螨类温度耐受性有关, 尤其是在螨类抵御高温胁迫中发挥重要作用 (Yang *et al.*, 2012; Xin *et al.*, 2018; Xu *et al.*, 2018; Tian *et al.*, 2020)。研究发现朱砂叶螨 *Tetranychus cinnabarinus* (Boiduval, 1956) 和柑橘全爪螨在 40℃ 高温胁迫下 *Hsp90* 基因表达量显著上调 (Feng *et al.*, 2010; 杨丽红等, 2016); 腐食酪螨和木薯单爪螨 *Mononychellus mcgregori* (Flechtmann *et Baker*, 1970) 在 42℃ 高温胁迫下 *Hsp70* 基因表达量提升 (卢芙蓉等, 2017; Wang *et al.*, 2021)。热激蛋白基因在螨类抗低温胁迫中也具有一定作用, 胡瓜新小绥螨在 5℃ 处理 6 h, *Hsp70* 和 *Hsp90* 基因表达上调 (Chen *et al.*, 2015)。朱砂叶螨于 4℃ 暴露 1 h 后, *Hsp90* 表达量增加 (Feng *et al.*, 2010)。然而, 由于螨类耐寒性调控机制的种间差异、热激蛋白基因家族间的功能差异, 使得热激蛋白对于螨类耐寒性的作用更为复杂。热激蛋白对于螨类耐寒性的影响仍需进一步探索。

## 4 总结与展望

耐寒性的研究是探讨螨类对低温适应机制的重要方面之一。当温度逐渐下降, 螨类是如何适应, 如何增强抗冻耐寒能力? 其中涉及复杂的基因水平和生理代谢水平的变化。目前螨类耐寒性的研究主要涉及过冷却点以及低温的胁迫作用等一部分生物学研究, 螨类耐寒性提升的生理代谢和分子调控机制亟待进一步研究。首先, 系统开展螨类低温抗逆性的研究, 包括不同螨类耐寒性类型的确定, 影响螨类过冷却点的因素等研究。第二, 在低温下, 昆虫维持体内稳态平衡的能力决定着抗寒性的高低, 因此昆虫的渗透调节能力对于耐寒性有重要的作用。螨类在低温下如何维持细胞内外的离子平衡需进一步研究。第三, 开

展螨类低温响应生理生化和代谢机制研究, 了解螨类在低温下代谢物质以及蛋白质 (酶) 的差异, 解析在螨类的耐寒性提升过程中发挥重要作用的小分子低温保护物质、保护酶、蛋白质的种类及变化。第四, 螨类耐寒性分子机制的研究, 解析螨类耐寒性提升的调控机制, 核心信号通路和相关基因的筛选, 关键基因的功能研究, 例如, 昆虫抗寒分子机制研究中的热点—热激蛋白基因、抗冻蛋白基因, 从分子水平揭示螨类耐寒性调控机制。

螨类耐寒性研究不仅对于阐明其对低温适应的分子机制有重要的理论意义, 而且对于探明害螨预测预报和综合防治具有重要的应用价值。首先, 了解螨类抗冻耐寒机制, 有利于揭示螨类越冬与存活规律, 预测其种群动态和潜在地理分布, 揭示害螨种群暴发成灾原因。其次, 通过对螨类耐寒性调控基因的研究, 可通过基因工程等相关技术开发新型生物制剂, 阻断害螨体内耐寒调控机制, 降低害螨抗寒能力, 减少越冬基数, 有效防治害螨。其三, 对于入侵害螨耐寒性的研究有助于揭示其入侵潜力和生态位转换的原因以及进化机制的探索。第四, 在捕食螨开发利用领域, 通过对捕食螨耐寒性调控机制的研究, 探索捕食螨低温耐受性提升的策略, 包括低温驯化, 滞育和低温保护物质的应用等策略, 延长捕食螨产品货架期, 降低捕食螨开发利用的成本, 促进捕食螨的商业化, 大力推动“以满治螨”的生物防治进程。

致谢: 感谢中国科学院东北地理与农业生态研究所刘冬研究员为马里恩海甲螨 *Halozetes marionensis* (Engelbrecht, 1974), 金黄海甲螨 *Halozetes fulvus* (Engelbrecht, 1975), 比利时海甲螨 *Halozetes belgicae* (Michael, 1903), 单奥甲螨属物种 *Phauloppia* sp., 南极阿拉斯加甲螨 *Alaskozetes antarcticus* (Michael, 1903) 5 种甲螨进行中文命名, 以及对为本文中的物种命名年代和中文名称进行的指导和修改。

## 参考文献 (References)

- Amani M, Khajehali J, Moradifaradonbeh M, *et al.* Species diversity of soil mites (Acari: Mesostigmata) under different agricultural land use types [J]. *Persian Journal of Acarology*, 2020, 9 (4): 353 - 366.
- Andreadis SS, Athanassiou CG. A review of insect cold hardiness and its

- potential in stored product insect control [J]. *Crop Protection*, 2017, 91: 93–99.
- Anthony SE, Sinclair BJ. Overwintering red velvet mites are freeze tolerant [J]. *Physiological and Biochemical Zoology*, 2019, 92 (2): 201–205.
- Bleiker KP, Smith GD. Cold tolerance of mountain pine beetle (Coleoptera: Curculionidae) pupae [J]. *Environmental Entomology*, 2019, 48 (6): 1412–1417.
- Block W, Duman DJG. Presence of thermal hysteresis producing antifreeze proteins in the Antarctic mite, *Alaskozetes antarcticus* [J]. *Journal of Experimental Zoology*, 1989, 250 (2): 229–231.
- Broufas GD, Koveos DS. Cold hardiness characteristics in a strain of the predatory mite *Euseius (Amblyseius) finlandicus* (Acari: Phytoseiidae) from Northern Greece [J]. *Annals of the Entomological Society of America*, 2001a, 94 (1): 82–90.
- Broufas GD, Koveos DS. Rapid cold hardening in the predatory mite *Euseius (Amblyseius) finlandicus* (Acari: Phytoseiidae) [J]. *Journal of Insect Physiology*, 2001b, 47 (7): 699–708.
- Brunetti C, Siepel H, Convey P, et al. Overlooked species diversity and distribution in the Antarctic mite genus *Stereotydeus* [J]. *Diversity*, 2021, 13 (10): 26.
- Bryon A, Kurlovs AH, Van Leeuwen T, et al. A molecular – genetic understanding of diapause in spider mites: Current knowledge and future directions [J]. *Physiological Entomology*, 2017, 42 (3): 211–224.
- Bryon A, Wybouw N, Dermauw W. Genome wide gene-expression analysis of facultative reproductive diapause in the two-spotted spider mite *Tetranychus urticae* [J]. *BMC Genomics*, 2013, 14 (1): 815.
- Chen H, Liang GM, Zou LY, et al. Research progresses in the cold hardiness of insects [J]. *Plant Protection*, 2010, 36 (2): 18–24. [陈豪, 梁革梅, 邹朗云, 等. 昆虫抗寒性的研究进展 [J]. *植物保护*, 2010, 36 (2): 18–24]
- Chen W, Li D, Zhang M, et al. Cloning and differential expression of five heat shock protein genes associated with thermal stress and development in the polyphagous predatory mite *Neoseiulus cucumeris* (Acari: Phytoseiidae) [J]. *Experimental and Applied Acarology*, 2015, 67 (1): 65–85.
- Clark MS, Worland MR. Cold insect review how insects survive the cold: Molecular mechanisms – a review [J]. *Journal of Comparative Physiology B – Biochemical Systemic and Environmental Physiology*, 2008, 178 (8): 917–933.
- Coombs MR, Bale JS. Thermal biology of the spider mite predator *Phytoseiulus macropilis* [J]. *Biocontrol*, 2014, 59 (2): 205–217.
- Deere JA, Sinclair BJ, Marshall DJ, et al. Phenotypic plasticity of thermal tolerances in five oribatid mite species from sub – Antarctic Marion Island [J]. *Journal of Insect Physiology*, 2006, 52 (7): 693–700.
- Des Marteaux LE, Hula P, Kostal V. Transcriptional analysis of insect extreme freeze tolerance [J]. *Proceedings of the Royal Society B – Biological Sciences*, 2019, 286 (1913): 20192019.
- Duman JG, Bennett V, Sformo T, et al. Antifreeze proteins in Alaskan insects and spiders [J]. *Journal of Insect Physiology*, 2004, 50 (4): 259–266.
- Eaton M, Kells SA. Freeze mortality characteristics of the mold mite *Tyrophagus putrescentiae*, a significant pest of stored products [J]. *Journal of Economic Entomology*, 2011, 104 (4): 1423–1429.
- Enriquez T, Colinet H. Cold acclimation triggers major transcriptional changes in *Drosophila suzukii* [J]. *BMC Genomics*, 2019, 20 (1): 1–17.
- Feng H, Wang L, Liu Y, et al. Molecular characterization and expression of a heat shock protein gene (*HSP90*) from the carmine spider mite, *Tetranychus cinnabarinus* (Boisduval) [J]. *Journal of Insect Science*, 2010, 10 (1): 1–14.
- Ghazy NA, Amano H. Rapid cold hardening response in the predatory mite *Neoseiulus californicus* [J]. *Experimental and Applied Acarology*, 2014, 63 (4): 535–544.
- Ghazy NA, Ohyama K, Amano H, et al. Cold storage of the predatory mite *Neoseiulus californicus* is improved by pre – storage feeding on the diapausing spider mite *Tetranychus urticae* [J]. *Biocontrol*, 2013, 59 (2): 185–194.
- Ghazy NA, Osakabe M, Negm MW, et al. Phytoseiid mites under environmental stress [J]. *Biological Control*, 2016, 96: 120–134.
- Ghazy NA, Suzuki T, Shah M, et al. Using high relative humidity and low air temperature as a long – term storage strategy for the predatory mite *Neoseiulus californicus* (Gamasida: Phytoseiidae) [J]. *Biological Control*, 2012, 60 (3): 241–246.
- Gotoh T, Akizawa T, Watanabe M, et al. Cold hardiness of *Neoseiulus californicus* and *Neoseiulus womersleyi* (Acari: Phytoseiidae) [J]. *Journal of the Acarological Society of Japan*, 2005, 14 (2): 93–103.
- Hart AJ, Bale JS, Tullett AG, et al. Effects of temperature on the establishment potential of the predatory mite *Amblyseius californicus* McGregor (Acari: Phytoseiidae) in the UK [J]. *Journal of Insect Physiology*, 2002, 48 (6): 593–599.
- Hatherly IS, Bale JS, Walters KFA, et al. Thermal biology of *Typhlodromips montdorensis*: Implications for its introduction as a glasshouse biological control agent in the UK [J]. *Entomologia Experimentalis et Applicata*, 2004, 111 (2): 97–109.
- Hawes TC, Bale JS, Worland MR, et al. Moulting reduces freeze susceptibility in the Antarctic mite *Alaskozetes antarcticus* (Michael) [J]. *Physiological Entomology*, 2007a, 32 (4): 301–304.
- Hawes TC, Bale JS, Worland MR, et al. Plasticity and superplasticity in the acclimation potential of the Antarctic mite *Halozetes belgicae* (Michael) [J]. *Journal of Experimental Biology*, 2007b, 210 (4): 593–601.
- Hill MP, Chown SL, Hoffmann AA. A predicted niche shift corresponds with increased thermal resistance in an invasive mite, *Halotydeus destructor* [J]. *Global Ecology and Biogeography*, 2013, 22 (8): 942–951.



- Ito K , Chae Y. Cold hardiness in immature stages and adults in the adult-diapausing spider mite *Stigmaeopsis longus* [J]. *Physiological Entomology* ,2019 ,44 ( 1 ): 11 – 19.
- Izadi H , Mohammadzadeh M , Mehrabian M. Cold tolerance of the *Tribolium castaneum* ( Coleoptera: Tenebrionidae ) , under different thermal regimes: Impact of cold acclimation [J]. *Journal of Economic Entomology* ,2019 ,112 ( 4 ): 1983 – 1988.
- Jensen K , Kristensen TN , Overgaard J , et al. Cold acclimation reduces predation rate and reproduction but increases cold – and starvation tolerance in the predatory mite *Gaeolaelaps aculeifer* Canestrini [J]. *Biological Control* ,2017 ,114: 150 – 157.
- Jensen K , Sørensen JG , Holmstrup M. Interactive effects of temperature and time on cold tolerance and spring predation in overwintering soil predatory mites ( *Gaeolaelaps aculeifer* Canestrini ) [J]. *Biological Control* ,2019 ,132: 169 – 176.
- Jiang CY , Wu Q , Yang NW , et al. The molecular regulation of diapause induction in insects [J]. *Chinese Journal of Applied Entomology* ,2021 ,58 ( 1 ): 1 – 13. [姜春艳 , 武强 , 杨念婉 , 等. 昆虫滞育诱导的分子调控机制 [J]. *应用昆虫学报* ,2021 ,58 ( 1 ): 1 – 13]
- Keosentse O , Mutamiswa R , Du Plessis H , et al. Developmental stage variation in *Spodoptera frugiperda* ( Lepidoptera: Noctuidae ) low temperature tolerance: Implications for overwintering [J]. *Austral Entomology* ,2021 ,60 ( 2 ): 400 – 410.
- Khodayari S , Colinet H , Moharrampour S , et al. Seasonal changes in the cold hardiness of the two – spotted spider mite females ( Acari: Tetranychidae ) [J]. *Environmental Entomology* ,2013a ,42 ( 6 ): 1415 – 1421.
- Khodayari S , Moharrampour S , Kamali K , et al. Effects of acclimation and diapause on the thermal tolerance of the two – spotted spider mite *Tetranychus urticae* [J]. *Journal of Thermal Biology* ,2012 ,37 ( 6 ): 419 – 423.
- Khodayari S , Moharrampour S , Larvor V , et al. Deciphering the metabolic changes associated with diapause syndrome and cold acclimation in the two – spotted spider mite *Tetranychus urticae* [J]. *PLoS ONE* ,2013b ,8 ( 1 ): e54025.
- Lu FP , Chen Q , Wu CL , et al. Influence of extreme high temperature exposure on protective enzymes and *Hsp70* gene expression of *Mononychellus mcgregori* ( Acari: Tetranychidae ) [J]. *Chinese Journal of Tropical Crops* ,2017 ,38 ( 5 ): 919 – 925. [卢芙蓉 , 陈青 , 伍春玲 , 等. 42℃ 极端高温胁迫对木薯单爪螨 (*Mononychellus mcgregori*) 保护酶及热激蛋白基因表达的影响 [J]. *热带作物学报* ,2017 ,38 ( 5 ): 919 – 925]
- Lubawy J , Chowanski S , Adamski Z , et al. Mitochondria as a target and central hub of energy division during cold stress in insects [J]. *Frontiers in Zoology* ,2022 ,19 ( 1 ): 1.
- Luybaert G , Witters J , Berkvens N , et al. Cold hardiness of the broad mite *Polyphagotarsonemus latus* ( Acari: Tarsonemidae ) [J]. *Experimental and Applied Acarology* ,2015 ,66 ( 1 ): 29 – 39.
- Masoumi Z , Shahidi Noghahi S , Izadi H. Trehalose and proline failed to enhance cold tolerance of the cowpea weevil , *Callosobruchus maculatus* ( F. ) ( Col. : Bruchidae ) [J]. *Journal of Stored Products Research* ,2021 ,93: 101853.
- Montiel PO. Profiles of soluble carbohydrates and their adaptive role in maritime Antarctic terrestrial arthropods [J]. *Polar Biology* ,1998 ,19 ( 4 ): 250 – 256.
- Moreau DL , Hardman JM , Kukul O. Supercooling capacity and survival of low temperatures by a pyrethroid-resistant strain of *Typhlodromus pyri* ( Acari: Phytoseiidae ) [J]. *Environmental Entomology* ,2000 ,29 ( 4 ): 683 – 689.
- Morewood WD. Cold hardiness of *Phytoseiulus Persimilis* Athias – henriot and *Amblyseius Cucumeris* ( Oudemans ) ( Acarina: phytoseiidae ) [J]. *Canadian Entomologist* ,1992 ,124 ( 6 ): 1015 – 1025.
- Qin M , Wang HF , Liu Z , et al. Research progress on insect resistance to cold and its mechanism [J]. *Apiculture of China* ,2017 ,68 ( 7 ): 21 – 24. [秦明 , 王红芳 , 刘振国 , 等. 蜜蜂耐寒性及其机理的研究进展 [J]. *中国蜂业* ,2017 ,68 ( 7 ): 21 – 24]
- Riddick EW , Wu Z. Potential long-term storage of the predatory mite *Phytoseiulus persimilis* [J]. *Biocontrol* ,2010 ,55 ( 5 ): 639 – 644.
- Shen ZL , Li YH , Zhou YT , et al. Review on the cold storage research of insect natural enemies [J]. *Chinese Journal of Tropical Crops* ,2017 ,38 ( 2 ): 374 – 380. [沈祖乐 , 李翌菡 , 周雅婷 , 等. 天敌昆虫低温贮藏研究进展 [J]. *热带作物学报* ,2017 ,38 ( 2 ): 374 – 380]
- Shi CH , Hu JR , Li CR , et al. Research progress in the cold tolerance mechanism of insects under environmental stress [J]. *Plant Protection* ,2016 ,42 ( 6 ): 21 – 28. [史彩华 , 胡静荣 , 李传仁 , 等. 环境胁迫下昆虫的耐寒适应机制研究进展 [J]. *植物保护* ,2016 ,42 ( 6 ): 21 – 28]
- Sinclair BJ , Alvarado LEC , Ferguson LV. An invitation to measure insect cold tolerance: Methods , approaches , and workflow [J]. *Journal of Thermal Biology* ,2015 ,53 ( 1 ): 180 – 197.
- Sitz RA , Peirce ES , Luna EK , et al. Temperature limits for the brown wheat mite , in Colorado [J]. *Journal of Economic Entomology* ,2019 ,112 ( 5 ): 2507 – 2511.
- Sjursen H , Sømme L. Seasonal changes in tolerance to cold and desiccation in *Phauloppia* spp. ( Acari , Oribatida ) from Finse , Norway [J]. *Journal of Insect Physiology* ,2000 ,46 ( 10 ): 1387 – 1396.
- Tang B , Lin QQ , Wu MJ , et al. The physiological regulation research of hardy proteins and induce insect's cold-resistance by cold acclimation [J]. *Journal of Environmental Entomology* ,2014 ,36 ( 5 ): 805 – 813. [唐斌 , 林青青 , 邹梦静 , 等. 抗寒类蛋白与冷驯化诱发昆虫耐寒的生理调节研究 [J]. *环境昆虫学报* ,2014 ,36 ( 5 ): 805 – 813]
- Teets NM , Denlinger DL. Surviving in a frozen desert: Environmental stress physiology of terrestrial Antarctic arthropods [J]. *Journal of Experimental Biology* ,2014 ,217 ( 1 ): 84 – 93.
- Teets NM , Kawarasaki Y , Potts LJ , et al. Rapid cold hardening protects against sublethal freezing injury in an Antarctic insect [J]. *Journal of Experimental Biology* ,2019 ,222 ( 15 ): jeb206011.
- Tian C , Li Y , Wu Y , et al. Sustaining induced heat shock protein 70 confers biological thermotolerance in a high – temperature adapted

- predatory mite *Neoseiulus barkeri* (Hughes) [J]. *Pest Management Science*, 2020, 77 (2): 939–948.
- Wang J, Que SQ, Liu XY, et al. Characteristic and expression of *Hsp70* and *Hsp90* genes from *Tyrophagus putrescentiae* and their response to thermal stress [J]. *Scientific Reports*, 2021, 11 (1): 1–12.
- Wang J, Que SQ, Xi JF, et al. Effect of temperature stress on the antioxidant capacity of *Tyrophagus putrescentiae* (Schrank) [J]. *Chinese Journal of Applied Entomology*, 2019, 56 (4): 687–693. [王静, 阙生全, 奚剑飞, 等. 温度胁迫对腐食酪螨抗氧化能力的影响 [J]. 应用昆虫学报, 2019, 56 (4): 687–693]
- White N, Bale JS, Hayward SAL. Life – history changes in the cold tolerance of the two – spot spider mite *Tetranychus urticae*: Applications in pest control and establishment risk assessment [J]. *Physiological Entomology*, 2018, 43 (4): 334–345.
- Worland MR, Leinaas HP, Chown SL. Supercooling point frequency distributions in Collembola are affected by moulting [J]. *Functional Ecology*, 2006, 20 (2): 323–329.
- Worland MR, LukesĽovaĽ A. The effect of feeding on specific soil algae on the cold-hardiness of two Antarctic micro-arthropods (*Alaskozetes antarcticus* and *Cryptopygus antarcticus*) [J]. *Polar Biology*, 2000, 23 (11): 766–774.
- Xin TR, Lian T, Li XY, et al. Gene cloning and expression of heat shock protein gene from *Aleuroglyphus ovatus* and its response to temperature stress [J]. *International Journal of Acarology*, 2018, 44 (7): 279–287.
- Xu YJ, Liu L, Yang Y, et al. Identification of four heat shock protein genes and their expression in response to thermal stress in two strains of *Neoseiulus barkeri* (Acari: Phytoseiidae) [J]. *Systematic and Applied Acarology*, 2018, 23 (4): 665–679.
- Yang LH, Dou W, Jiang HB, et al. Cloning and expression profiling of heat shock protein gene *PcHsp90* in the citrus red mite, *Panonychus citri* (Acari: Tetranychidae) [J]. *Acta Entomologica Sinica*, 2016, 59 (4): 411–420. [杨丽红, 豆威, 蒋红波, 等. 柑橘全爪螨热激蛋白基因 *PcHsp90* 的克隆及表达模式分析 [J]. 昆虫学报, 2016, 59 (4): 411–420]
- Yang L, Jiang H, Liu Y, et al. Molecular characterization of three heat shock protein 70 genes and their expression profiles under thermal stress in the citrus red mite [J]. *Molecular Biology Reports*, 2012, 39 (4): 3585–3596.
- Yue L, Guo JY, Zhou ZS, et al. Effects of cold acclimatization on insect cold hardiness and fitness [J]. *Chinese Journal of Biological Control*, 2013, 29 (2): 286–293. [岳雷, 郭建英, 周忠实, 等. 冷驯化对昆虫耐寒性及其适合度的影响 [J]. 中国生物防治学报, 2013, 29 (2): 286–293]
- Zhang GH, Liu H, Wang JJ, et al. Effects of thermal stress on lipid peroxidation and antioxidant enzyme activities of the predatory mite, *Neoseiulus cucumeris* (Acari: Phytoseiidae) [J]. *Experimental and Applied Acarology*, 2014, 64 (1): 73–85.
- Zhang XX, Iqbal J, Dou YZ. Advances in research on the rapid cold hardening of insects [J]. *Chinese Journal of Applied Entomology*, 2021, 58 (2): 256–264. [张小香, Iqbal J, 杜予州. 昆虫快速冷耐受的研究进展 [J]. 应用昆虫学报, 2021, 58 (2): 256–264]
- Zhigulskaia ZA, Berman DL. Cold-hardiness of the phoretic mites *Anoetus myrmicarum* (Acariformes, Anoetidae) from the ants *Formica lemani* (Hymenoptera, Formicidae) in the Kolyma Highland [J]. *Entomological Review*, 2014, 94 (6): 920–924.