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2000 年以来中国昆虫滞育研究进展与展望*

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摘　要　自 1933 年家蚕与蝗虫卵滞育的光周期调控被首次揭示以来，昆虫滞育研究已历经 90 多年的学术积淀。本文聚焦 2000 年以来国内昆虫滞育研究前沿，系统综述了昆虫滞育调控的核心科学问题研究进展与前沿案例：（1）滞育的环境生态学调节机制；（2）滞育发育动态的生理代谢规律；（3）卵（胚胎）、幼虫、蛹和成虫不同虫态滞育的分子调控机制。展望了今后昆虫滞育基础理论和应用实践研究发展的方向。深化滞育调控机制解析将有助于发掘基于滞育操控的新型分子靶标、构建基于滞育特性的种群基数监测模型，优化重大害虫生态管理策略，也可为传粉昆虫、天敌昆虫和资源昆虫的保育利用提供滞育调控理论依据。本综述旨在为昆虫滞育研究的理论创新与应用转化提供系统性参考。

关键词　昆虫滞育；环境因素调节；生理代谢调节；分子机制；代谢通路；调控网络

Progress in research on insect diapause in China since 2000

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Abstract　Since the elucidation of the photoperiodic regulation of diapause in the eggs of the silkworm, *Bombyx mori*, and in the locust, *Acrydium arenosum*, in 1933, there have been over 90 years of research on insect diapause. This review summarizes the core scientific advancements in research on the regulation of insect diapause in China since the beginning of the 21st century, including: (1) Physiological and ecological mechanisms involved in environmental factors of photoperiod-temperature synergy; (2) Physiological metabolic regulation during diapause induction, maintenance, and termination; (3) Molecular switch mechanisms across different developmental stages (egg/embryonic, larval, pupal, and adult diapause). Prospects for future research are also presented. Deepening mechanistic understanding of diapause regulation will facilitate: (a) The discovery of novel molecular targets for diapause-based pest management; (b) The development of population monitoring models based on diapause characteristics; (c) The optimization of ecological management strategies for major pests, while at the same time, providing a theoretical foundation for the conservation and utilization of beneficial pollinators, predatory and parasitic insects, and other insect resources. This review aims to offer comprehensive references for both theoretical and applied research on insect diapause.

Key words　insects diapause; environmental factors regulation; physiological metabolism regulation; molecular mechanism; metabolic pathway; regulation network

昆虫在长期进化选择过程中，对环境逆境条件形成了两种适应性选择策略：迁飞（Migration）——从空间上的拓展选择适宜生长、发育或繁殖的栖息地；蛰伏（Dormancy，包含休眠（Quiescence）和滞育（Diapause））——从时间上的逃避不良的环境条件。两种适应性生态对策有利于昆虫种群扩展时间生态位和空间生态位，提升昆虫在严酷逆境条件下存活（Tauber *et al*., 1986; Danks, 1987; Denlinger, 2002; Hickmann *et al*., 2025）。昆虫滞育的生态生

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理特性构成了昆虫整个生活史的基础，将昆虫的发育/繁殖阶段与最有利的寄主、取食、发育、交配和繁殖等时机同步，对昆虫种群基数的形成、维持与延续，种群的存活、发育、生殖与适应进化都具有重要的生理生态学意义（Tauber *et al*., 1986; Danks, 1987; Denlinger, 2002, 2022; Koštál, 2006; Hickmann *et al*., 2025）。

昆虫滞育是一系列的动态生理过程，受昆虫分子遗传特性、内分泌生理生化和光周期、温度等外部生态环境因素的综合调节。2000 年之前，我国昆虫滞育相关研究主要围绕越冬越夏的生物学特性、滞育关键酶活性、昆虫滞育的内分泌（蜕皮激素、保幼激素、促前胸腺激素、滞育激素）调节、滞育激素（Diapause hormone, DH）的生理、滞育激素和性信息素合成激活肽（Diapause hormone and pheromone biosynthesis-activating neuropeptide, DH-PBAN）基因克隆与表达取得系列进展（徐卫华，1999）。2000 年以来，昆虫滞育环境生理生态学调节机制（光温反应、光周期钟和光周期时间测量特性、滞育地理变异）、滞育生理生化代谢调节机制和滞育分子开关与互作调节网络等方面受到昆虫适应性进化理论研究、害虫种群监测与高效绿色防控、益虫合理利用等应用昆虫学研究的高度重视。美国 David L. Denlinger 教授 2022 年出版《Insect Diapause》，对国际昆虫滞育的发展和动态进行了非常系统的总结（Denlinger, 2022）。国内 2000 年以来昆虫滞育的研究从生理生态领域逐步深入，滞育相关能量、激素、生殖代谢的生理生化与滞育分子调节机制，结合后基因组时代多组学技术、从代谢通路网络调控、分子互作调控和遗传机制解析等水平开展了多尺度的系统研究。

基于中国知网（China National Knowledge Infrastructure, CNKI）和 Web of Science 科学引文索引（Science Citation Index Expanded, SCIE）数据库，检索 2000-2025 年以主题为“Diapause or diapausing or diapaused”我国学者发表的 SCI 收录论文共 645 篇，呈年度增长态势；CNKI 收录论文 1 590 篇（图 1）。2000 年以来，有学者综述了昆虫滞育的研究进展（王满囷和李周直，2004; 徐卫华, 2008; 张晓燕等, 2015），亦有对小麦吸浆虫（仵均祥等，2004）、蝴蝶（易传辉等，2007）、赤眼蜂（张俊杰等，2009; Shen *et al*., 2025）、寄生蜂（张礼生等，2014; 张洪志等，2018）、草蛉（王曼姿等, 2019）、家蚕 *Bombyx mori*（蒋涛等, 2017）、伊蚊（马敏等, 2018）、熊蜂（Shi *et al*., 2023）等昆虫的滞育研究进行了系统梳理。

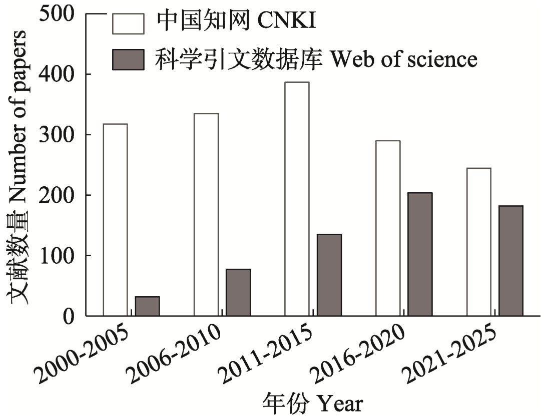

图 1　2000-2025 年中国昆虫滞育研究发表的论文数量（来源于 CNKI 和 Web of Science）

Fig. 1　The number of papers published on the topic of insect diapause during 2000 to 2025 in China (data from CNKI and Web of Science)

本文系统概述国内 2000 年以来昆虫滞育的环境因素调节机制、滞育的生理生化代谢调节机制和不同滞育类型（虫态）的分子调节机制等方面的研究进展与前沿案例，以期为基于滞育种群基数监测预警、害虫生态治理和绿色防控分子靶标发掘提供理论参考；也可为传粉昆虫、天敌昆虫和资源昆虫的合理利用提供科学依据。

1　滞育的环境因素调节机制

围绕光周期、温度、湿度、营养等环境因素对昆虫滞育的调节进行了大量的研究，特别是光周期和温度对昆虫滞育诱导、维持、解除和滞育后发育的调节有较系统的研究。

1.1　昆虫滞育的光温反应

滞育环境生态调节因子中，光周期是最稳定、最可靠和最准确的季节信号。大量研究揭示滞育诱导的光周期反应类型、诱导种群 50%

个体滞育的临界光周期和不同光温反应诱导滞育比率与滞育持续期差异。昆虫滞育诱导的光周期反应可分为长日照反应型（二化螟 *Chilo supperssalis*、环带锦斑蛾 *Pseudopidorus fasciata*、亚洲玉米螟 *Ostrinia furnacalis* 等）、短日照反应型（大猿叶虫 *Colaphellus bowringi*）、短日照-长日照反应型（大菜粉蝶 *Pieris brassicae*）和中间型日长反应型（黑纹粉蝶 *Pieris melete*）（肖海军等, 2004）。

夏季滞育通常认为由长光照和高温诱导（刘柱东等, 2002），冬季滞育则通常认为由短光照和低温诱导。但有研究表明，夏季滞育和冬季滞育诱导对温度的响应有多种途径。如大猿叶虫为世界上首例证明由低温与长光照诱导的夏季滞育（Xue *et al*., 2002），而二化螟自然种群冬季滞育由高温配合逐渐缩短的光周期诱导（Xiao *et al*., 2010）。根据昆虫滞育临界日长受温度影响的程度，将光温反应的分为温度敏感和温度补偿两类（肖海军等, 2004）。温度补偿型光温反应，滞育诱导主要取决于光周期，温度的作用较小，生态范围内的温度对临界光周期影响较小（Xiao *et al*., 2010）。温度敏感型则温度显著影响滞育的诱导，特别对临界日长有显著调节作用（Xiao *et al*., 2008）。

1.2 昆虫滞育的光周期钟与时间测量机制

昆虫滞育的光周期钟的研究主要通过共鸣实验和 Bünsow 试验判断昆虫滞育光周期钟的性质：如曲线呈现以接近 24 h 为间隔周期的高峰或低谷为正反应（Positive response），反之则为负反应（Negative response）。国内现有研究模型主要支持非昼夜节律的沙漏钟（Noncircandian oscillator hourglass clock）模型（表 1），仅有大猿叶虫呈现部分昼夜节律钟（Circadian clock）。昼夜节律钟与沙漏钟的特征差异表现在昼夜节律钟在延长的极端长暗期，仍按 24 h 左右的周期测量时长；相反，沙漏钟则在延长的暗期仅进行一次时间测量，需要一个光期刺激方能重启计时。

表 1　昆虫滞育的光周期钟研究

Table 1　Studies on photoperiodic regulation on insect diapause

昆虫 Insect	诱导/解除 Induction/ termination	测量光期/暗期 Measurement light/Dark	共鸣实验 Resonance experiment	Bünsow 实验 Bünsow experiment	光周期钟模型 Photoperiodic clock model	文献 Reference
环带锦斑蛾 *Pseudopidorus fasciata*	滞育诱导 Diapause induction	暗期 Scotophase	负反应 Negative	负反应 Negative	沙漏钟 Hourglass	Wei *et al*., 2001
二化螟 *Chilo suppressalis*	滞育诱导 Diapause induction	暗期 Scotophase	负反应 Negative	负反应 Negative	沙漏钟 Hourglass	Chen *et al*., 2011
大猿叶虫 *Colaphellus bowringi*	滞育诱导 Diapause induction	暗期 Scotophase	正反应 Positive	负反应 Negative	部分昼夜节律 Partly circadian	Wang *et al*., 2004
黑纹粉蝶 *Pieris melete*	滞育诱导 Diapause induction	暗期 Scotophase	负反应 Negative	负反应 Negative	沙漏钟 Hourglass	Xiao *et al*., 2009
马尾松毛虫 *Dendrolimus punctatus*	滞育诱导 Diapause induction	暗期 Scotophase	负反应 Negative	负反应 Negative	沙漏钟 Hourglass	Huang *et al*., 2005
油松毛虫 *Dendrolimus tabulaeformis*	滞育诱导 Diapause induction	暗期 Scotophase	负反应 Negative	负反应 Negative	沙漏钟 Hourglass	Han *et al*., 2005
亚洲玉米螟 *Ostrinia furnacalis*	滞育诱导 Diapause induction	暗期 Scotophase	负反应 Negative	负反应 Negative	沙漏钟 Hourglass	Yang *et al*., 2014
条纹小斑蛾 *Thyrassia penangae*	滞育诱导 Diapause induction	光期 Photophase	负反应 Negative	负反应 Negative	沙漏钟 Hourglass	He *et al*., 2009
环带锦斑蛾 *Pseudopidorus fasciat*	滞育解除 Diapause termination	暗期 Scotophase	负反应 Negative	负反应 Negative	沙漏钟 Hourglass	Li *et al*., 2003

光周期时间测量也存在两种机制，一是昆虫测量光周期显示全有或全无的反应，即质量反应（Qualitative response），如环带锦斑蛾诱导 50%个体进入滞育的光暗循环数、滞育的强度相对稳定（Hua *et al*., 2005）。另一种是昆虫可以准确地测量光周期的实际长度，不同的光周期有不同的滞育诱导效应，即数量反应（Quantitative response），如大猿叶虫诱导 50%个体进入夏季滞育的光暗循环数差异较大、不同光周期诱导滞育的强度差异显著（刘兴平等, 2009）。黑纹粉蝶夏季滞育诱导的光周期时间测量为数量反应，而冬季滞育诱导光周期时间测量为数量反应（Xiao *et al*., 2008, 2012）。

1.3 昆虫滞育环境响应的地理变异特点

昆虫滞育的虫态、光周期反应、光敏感阶段、诱导滞育的比率、临界光周期、滞育持续期、滞育后的繁殖等性状可呈现地理种群差异（孙莉等, 2007）。系统比较 6 个不同地理种群亚洲玉米螟滞育诱导的光周期反应，临界光周期、光敏感期和滞育持续期，发现广西阳朔、江西南昌、山东泰安、河北廊坊和黑龙江哈尔滨种群的光周期反应为长日照型，滞育率、临界光周期与滞育持续期和种群地理纬度呈正相关关系，而海南乐东种群在 25-31 ℃下缺乏光周期反应，22 ℃显示了较弱的光周期反应（Huang *et al*., 2013, 2020; Xie *et al*., 2015）。棉铃虫 *Helicoverpa armigera* 不同地理种群的滞育诱导的临界光周期变化与种群的地理纬度起源呈正相关。北方和南方种群对光周期和温度诱导滞育反应差异显著，北方种群对光周期高度敏感，而南方种群对温度高度依赖（Chen *et al*., 2013）。灰飞虱 *Laodelphax striatellus*、丝带凤蝶 *Sericinus montelus*、小菜蛾盘绒茧蜂 *Apanteles plutellae* 等滞育诱导地理变异均显示滞育率、临界光周期、滞育持续期与地理纬度呈正相关趋势（Ahmed *et al*., 2007; Wang *et al*., 2012; Hou *et al*., 2016）。

以不同地理种群之间杂交或回交实验，根据后代的滞育率表型，以是否符合加性模型分析滞育的地理种群遗传特点。先后在大猿叶虫、棉铃虫、亚洲玉米螟等昆虫中进行了不同地理种群杂交与回交实验。如棉铃虫杂交 F_1 代滞育率和滞育持续期介于其亲本之间，父本在滞育决定中扮演更重要的角色（Chen *et al*., 2012a）。大猿叶虫在 12 和 13 h 光照下，F_1 代的滞育率介于其亲本之间，光周期诱导滞育受母本基因型影响，母本对滞育诱导的影响大于父本（Chen *et al*., 2014）。亚洲玉米螟以滞育种群作为父本或祖父本的杂交后代滞育率最高，而以非滞育种群作为父本或祖父本的后代滞育率最低，表明父本对后代滞育率的影响大于母本，滞育遗传不符合加性模型，以不完全显性方式遗传，亲本和遗传-环境互作共同参与亚洲玉米螟滞育地理变异调节（Xia *et al*., 2012; Huang *et al*., 2013, 2020; Fu *et al*., 2015; Xiao *et al*., 2015b）。

2 滞育的生理代谢调节

滞育同时伴随生理、代谢、表型等方面的变化，以应对不利环境。昆虫滞育的生理主要表现为呼吸代谢下降，显著降低耗氧量；虫体含水量下降、脂肪存储量增加；积累海藻糖、甘油等抗冻物质，关键酶系活性减弱、分子伴侣等抗逆蛋白增强等（Denlinger, 2022）。

2.1 呼吸代谢

昆虫在滞育期间呼吸代谢显著降低。如烟青虫 *Helicoverpa assulta* 夏滞育蛹的代谢率始终低于非滞育蛹，且受滞育状态和蛹龄共同影响（Liu *et al*., 2016b）。柞蚕 *Antheraea pernyi* 滞育约 1 个月后呼吸代谢率降至最低（Wang *et al*., 2021）。哈氏啮小蜂 *Habrobracon hebetor* 在 20 ℃和 10L：14D 下饲养的雌蜂产卵前期较 16L：8D 下显著延长，且呼吸速率更低（Chen *et al*., 2012b）。黑纹粉蝶滞育蛹呼吸代谢释放的 CO_2 较非滞育蛹显著减少（吴珍平等, 2019）。黑纹粉蝶夏滞育和冬滞育期间的呼吸代谢监测，其呼吸代谢速率呈“U”型曲线，滞育初期呼吸代谢速率水平相对较高，滞育期的呼吸代谢速率最低，到滞育后期部分个体的呼吸代谢水平再次升高（吴珍平, 2019）。

2.2 能量代谢

昆虫滞育期间的糖类、醇类、脂类和氨基酸等能量代谢至关重要。以卵（胚胎）或蛹滞育的昆虫，滞育期间无法补充取食，其所有的能量代谢营养物质均来源于母体或滞育前发育阶段的营养储备。在滞育准备期，注定滞育的个体通常降低含水量、大量积累甘油、脂肪、海藻糖等能源物质，以满足后续整个滞育进程中能量需求。如丝带凤蝶（Wang *et al*., 2007）、黑纹粉蝶（Xiao *et al*., 2015a）、柞蚕（Li *et al*., 2020）、葱地种蝇 *Delia antiqua*（Guo *et al*., 2015），菜蛾绒茧蜂 *Cotesia vestali*（Hao *et al*., 2015）、美国白蛾 *Hyphantria cuneas*（Wang *et al*., 2023）等均在滞育准备期显著降低含水量，滞育蛹大量积累能源与营养物质。滞育解除及解除后的发育阶段，海藻糖分解代谢增强，海藻糖转化为糖原（Li *et al*., 2020）。部分在滞育期间可补充取食的昆虫，滞育期间是否取食在个体或昆虫种类间差异很大。海藻糖在滞育过程中扮演着能量来源和逆境保护剂的关键角色。滞育过程中，昆虫体内的糖类之间可以互相转化，如糖原和海藻糖的含量变化趋势呈典型的“镜像关系”。麦红吸浆虫 *Sitodiplosis mosellana* 的海藻糖水平在进入滞育时大幅增加，在低温滞育期达到峰值，并在滞育后发育阶段显著下降，且与海藻糖合成酶活性变化高度一致，而与海藻糖降解酶活性表现出完全相反的模式（Huang *et al*., 2021）。滞育期间的温度等环境条件显著影响能量物质代谢。如熊蜂 *Bombus terrestris* 蜂王滞育前采用低温驯化，既增加脂质的积累，又降低滞育期内蛋白、脂质和总糖的消耗（Shi *et al*., 2023）。总体上，滞育准备期所储备的能量代谢物质对滞育期间及滞育后发育的能量代谢需求至关重要。

2.3 激素代谢

诱导和解除滞育的外部环境因素，须通过体内神经分泌系统才发挥功能。昆虫内激素互作网络调节昆虫滞育，滞育激素和信息素合成激活神经肽（DH-PBAN）是与滞育相关的神经肽（Zhang *et al*., 2004a）。昆虫脑中促前胸腺激素神经元分泌激素，活化咽下神经节，分泌滞育激素，诱导卵滞育（徐卫华, 1999; Zhang *et al*., 2004a）。昆虫脑中促前胸腺激素神经元分泌的激素减少，无法活化前胸腺，蜕皮激素缺乏，使幼虫和蛹的变态发育受到抑制而诱导滞育幼虫和滞育蛹。脑神经元减少了促咽侧体素的分泌，咽侧体不被活化，保幼激素缺乏，性腺和性细胞发育受阻诱导生殖滞育（徐卫华, 1999; 徐晶晶等, 2012）。神经内分泌细胞分泌的神经肽类激素为上游调控激素，调节下游激素的合成和分泌来调节滞育或发育（Wei *et al*., 2005）。保幼激素和蜕皮激素是主要的下游激素受神经肽类的调控（高俏等, 2018）。

昆虫变态与滞育阶段的精确时序受激素调控。现有研究支持促前胸腺激素（Prothoracicotropic hormone, PTTH）、蜕皮激素（Ecdysterone, 20E）、保幼激素（Juvenile hormone, JH）和滞育激素（Diapsuse hormone, DH）等的滴度与滞育调节密切相关。家蚕胚胎滞育由 DH 诱导（Zhang *et al*., 2004a），蜕皮激素参与调控（Zhu *et al*., 2019a）。草地螟 *Loxostege sticticalis* 幼虫在滞育诱导、滞育维持和滞育解除过程中血淋巴保幼激素（JH Ⅰ）滴度动态变化，高水平 JH 滴度促进幼虫滞育诱导和维持，JH 滴度降低则导致幼虫滞育解除（Jiang *et al*., 2011）。RNAi 敲低灰飞虱若虫保幼激素酸甲基转移酶 JHAMT 与蜕皮激素合成酶 CYP314A1（*Shd*）后，血淋巴 JH III 与 20E 滴度显著下降，若虫发育历期显著延长，证实 JH 和 20E 合成酶通过调控激素滴度决定若虫滞育（Zhai *et al*., 2017）。柞蚕蛹滞育解除及滞育后发育阶段，血淋巴中内源性 20-羟基蜕皮酮（20E）水平升高, 20E 在滞育解除及滞育后发育控制海藻糖分解代谢中有重要作用（Li *et al*., 2020）。菜粉蝶滞育蛹中 20-羟基蜕皮酮（20E）滴度低于非滞育型蛹，滞育蛹用 20E 处理可打破滞育（Liao *et al*., 2024）。棉铃虫滞育激素的功能并非诱导滞育，而是促进蛹发育，能够打破蛹滞育（Zhang *et al*., 2004c）。烟实夜蛾 *Helicoverpa assulta* 咽下神经节神经肽 I（Has-SGNP1）和棉

铃虫滞育激素结构类似，也是蛹滞育终止激素（Zhao *et al*., 2004）。棉铃虫促前胸腺激素 mRNA 在非滞育蛹中高表达，滞育蛹中低表达，滞育解除时再度升高，重组 PTTH 亦可成功打破蛹滞育（Wei *et al*., 2005）。在注定滞育与非滞育蛹血淋巴中，3 日龄前 PTTH 滴度相似，4 日龄后差异显著，可在调控棉铃虫蛹滞育中起关键作用（Hou and Xu, 2007）。

保幼激素（JH）滴度的降低已被证明是诱导昆虫生殖滞育的共同内分泌机制，在短光照下饲养的异色瓢虫 *Harmonia axyridis*，JH 滴度显著较低，雄性内生殖系统发育相对不成熟，JH 的缺乏引起生殖滞育的诱导和维持，JH 生物合成途径决定滞育雌虫 JH 滴度的降低（Gao *et al*., 2022a, 2022b）。羽化后第 4 天的大猿叶虫雌成虫，非滞育雌虫体内 20E 滴度显著高于滞育雌虫（Guo *et al*., 2021）。草地螟组蛋白去乙酰化酶（Histone deacetylase, HDAC）在诱导滞育的光周期下调控幼虫体内的 JH 含量，通过改变 JH 水平参与调节滞育（Cui *et al*., 2022）。

2.4 酶代谢

昆虫滞育过程中，过氧化物、过氧化氢等保护酶系统、海藻糖代谢酶、组蛋白去乙酰化酶等代谢活性参与滞育的调节。麦红吸浆虫幼虫过氧化物酶（Peroxidase, POD）、超氧化物歧化酶（Superoxide dismutase, SOD）和过氧化氢酶（Catalase, CAT）保护酶活性，从滞育前到滞育初期保护性酶的活性呈下降趋势，酶活性随着滞育后幼虫的发育逐渐增加（成卫宁等, 2008）。海藻糖合成酶的活性在进入滞育时大幅增加，滞育期间达到峰值，在滞育后发育阶段显著下降，而海藻糖降解酶的活性呈完全相反的模式（Huang *et al*., 2021）。菜蛾盘绒茧蜂 *Cotesia vestalis* 非滞育预蛹和成虫中的过氧化氢含量、超氧化物歧化酶和过氧化物酶活性均随着光周期的缩短而下降，而过氧化氢酶活性显著增加。与滞育预蛹相比，葱蝇 *Delia antiqua* 非滞育预蛹具有显著更高的超氧化物歧化酶、更低的过氧化氢酶和相似的过氧化物酶活性（Hao *et al*., 2012）。短光照诱导菜蛾盘绒茧蜂糖原合酶活性显著升高；糖原磷酸化酶的活性在卵期显著更高，预蛹期显著降低，其他阶段含量稳定（Hao *et al*., 2013）。注射牛胰岛素，可诱导柞蚕滞育解除和同步羽化，并上调海藻糖酶的表达，提高可溶性与膜结合海藻糖酶活性，诱导血淋巴海藻糖水平下降（Li *et al*., 2021b）。灰飞虱滞育若虫过冷却点显著降低，海藻糖酶、丙酮酸激酶及山梨醇脱氢酶活性均降低（Zhai *et al*., 2018）。

3 滞育的分子调节机制

随着多组学与基因编辑等分子生物学技术的发展，国内昆虫滞育的分子调节、信号通路方面有丰富的研究案例，主要集中在不同虫态昆虫滞育过程中的光温感受调节、能量代谢、内分泌代谢、生物钟、胰岛素等多种信号途径相关的基因（蛋白）功能与调控网络。

3.1 卵（胚胎）滞育

国内对卵（胚胎）滞育调控机制的研究主要集中于家蚕和东亚飞蝗 *Locusta migratoria*。家蚕滞育发生在胚胎期，由滞育激素（DH）、昼夜节律钟和多种信号通路调控（Zhang *et al*., 2004a; Chen *et al*., 2022; Fan *et al*., 2023）。胰岛素/IGF 信号（IIS）通路在滞育昆虫的寿命、能量积累和抗逆性调控中至关重要，胰岛素受体（*BmINR*）及其下游基因腺苷酸环化酶 6（*BmAC6*）通过胰岛素/IGF 信号通路调控家蚕的胚胎滞育（Fan *et al*., 2023）。对滞育和非滞育卵巢比较转录组揭示过氧化物酶代谢、三酰甘油积累、抗冻剂和蜕皮激素生物合成等在滞育组上调（Chen *et al*., 2017）。对注射 DH 后 4 和 12 h 的卵巢转录组测序，鉴定出的差异表达基因主要涉及内分泌激素合成代谢、细胞解毒、核糖体蛋白、脂质代谢和表观遗传修饰（Chen *et al*., 2022）。RNA m^6A 甲基化通过调节二羟丙酮磷酸酰基转移酶（DHAPAT）和磷脂酸磷酸酶（PAP）基因的表达，m^6A 表观遗传修饰可结合脂质代谢信号通路参与滞育的调控（Chen *et al*., 2023a）。家蚕昼夜节律基因 *Period* 转录翻译反馈环可调节滞育激

素水平，敲除 *Period* 基因的突变体昼夜节律钟系统转录翻译反馈环受损，通过改变 *Cycle* 的表达水平直接上调 GABA 受体 GRD 的表达，持续激活 GABA-ergic 信号，抑制 DH 释放至血淋巴。因此，生物钟通过 GABA-DH 神经递质-内分泌激素 DH 途径，降低 DH 的滞育诱导效应（Cui *et al*., 2021）。miRNA 能够响应滞育诱导温度，通过调控昼夜节律基因参与调节滞育，如 *bmo-miR-6497-3p* 可直接靶向调控昼夜节律基因 *Cycle* 表达，参与胚胎滞育诱导的调控（Liu *et al*., 2021）。通过正向遗传学手段，以受温度诱导的兼性滞育品系和非滞育品系为亲本构建作图群体，将调控滞育变异的主效位点定位至 Z 染色体末端，并将关键变异位点定位在该区域内 *Cycle* 基因的 5′端。*Cycle* 基因通过可变剪接编码 3 个亚型（Isoforms A-C）。非滞育品系在 C 亚型特异的 N 端外显子上存在 1-bp 的碱基缺失，导致 C 亚型发生整体性移码突变。CYC-C 亚型可能作用于 GABAergic-Corazonin-DH 通路调控家蚕滞育的环境诱导，而 A/B 亚型发挥 CYC 本身的昼夜节律调控功能（Zheng *et al*., 2025）。

比较转录组测序和蛋白质组检测到东亚飞蝗滞育卵和非滞育卵的大量差异表达转录本和差异表达蛋白点，差异转录本和蛋白点中的大多数在滞育处理中上调，且与保幼激素生物合成、胰岛素和过氧化物酶体信号通路相关联（Hao *et al*., 2017; Cui *et al*., 2019）。丝氨酸蛋白酶抑制剂基因 *LmSPN2* 和 *LmSPN3* 通过 Toll 通路共同调控东亚飞蝗的胚胎滞育（Feng *et al*., 2023）。东亚飞蝗胰岛素信号通路中的 *LmPrx6* 被敲低时，滞育率显著降低，糖原合酶和磷酸烯醇式丙酮酸羧激酶（Phosphoenolpyruvate carboxykinase, PEPCK）表达下调，*LmPTP1B* 的磷酸化水平显著降低，而 *LmIR*、*LmAKT* 和 *LmFOXO* 的磷酸化水平显著增加。沉默 *LmPrx6* 后，增强应激耐受性的过氧化氢酶和 Mn 超氧化物歧化酶（Mn-SOD）mRNA 表达显著下调（Chen *et al*., 2020）。在短日照条件下，东亚飞蝗雌成虫的蛋白酪氨酸磷酸酶 PTP1B 诱导卵滞育，而蛋白酪氨酸激酶 PTK 则抑制卵滞育；抗氧化酶 Prx Ⅴ可负向调控 NADPH 氧化反应，显著降低 ROS 生成和 NADPH-OX 活性。雌成虫的 PTP1B、PTK 及 Prx Ⅴ通过胰岛素信号通路充当上游调控因子，在短日照下决定子代卵是否滞育（Li *et al*., 2021a）。

3.2 幼虫滞育

幼虫滞育显著受蜕皮激素、保幼激素和能量代谢与抗逆相关基因的调节。高温能有效促进松墨天牛 *Monochamus alternatus* 幼虫滞育终止，而滞育前 Ca^{2+}的添加能显著加快滞育的解除，Ca^{2+}的添加调节 20E、JH 生物合成和降解相关基因的表达，通过介导 20E 和 JH 的生物合成和降解来调节滞育（Yang *et al*., 2023）。亚洲玉米螟幼虫滞育相关糖原磷酸化酶基因 *Ofgp* 的表达模式研究发现，非滞育幼虫血淋巴 *Ofgp* 转录水平最高，滞育幼虫脂肪体的转录水平最高，滞育越冬期间表达水平持续增加，转录水平与环境温度呈负相关（Guo *et al*., 2016）。

昆虫滞育通常诱导滞育关联蛋白的上调表达（肖海军等, 2011）。麦红吸浆虫在不同滞育发育阶段幼虫差异蛋白质组分析，夏滞育、冬滞育和滞育后发育阶段，分别诱导 91、92 和 95 个蛋白点丰度上调 2 倍以上（Cheng *et al*., 2009）。麦红吸浆虫 *hsp70* 和 *hsp90* 的表达受滞育诱导，*hsp70* 在夏季的表达比冬季更强，而 *hsp90* 则表现出相反的模式，*hsc70* 在滞育前和滞育期间表达稳定，在滞育后静息期显著上调（Cheng *et al*., 2016）。二化螟 16 种小分子热激蛋白的差异表达检测，发现 *Cshsp19.8*、*Cshsp21.4*、*Cshsp21.5* 的表达水平在二化螟解除滞育期都呈显著下调，而 *Cshs p90*、*Cshsp70* 和 *Cshsp60* 表达与二化螟幼虫滞育有紧密关联（Lu *et al*., 2013, 2014）。HSP/共伴侣网络的激活依赖于越冬幼虫的滞育状态，冷驯化可进一步提高滞育幼虫的耐寒性（Jiang *et al*., 2021a）。亚洲玉米螟 HSP70 基因家族和蛋白酶体通路在幼虫滞育期呈现动态变化，用 HSP 激活剂/抑制剂及蛋白酶体抑制剂调控蛋白水平，可显著影响滞育进程（Yang *et al*., 2024）。大豆食心虫 *Leguminivora glycinivorella* 应用RNAi敲降脂肪酸合成酶基因降低滞育幼虫

存活率；小分子热激蛋白 *HSP19.8*/*18.9* 敲降使约50%幼虫解除滞育，说明 *FAS* 与 *sHSPs* 参与滞育维持的调节（Yang *et al*., 2020）。

应用泛基因组、群体转录组、QTL 定位等方法，揭示了亚洲玉米螟基因组的结构变异（SVs）显著影响启动子活性，并调节幼虫的发育历期，揭示基因组的结构变异在滞育等适应性进化中的作用（Peng *et al*., 2024）。对 7 个种群全基因组测序（Pool-seq）揭示数百个单核苷酸多态性（SNP）的等位基因频率响应滞育临界光周期、滞育后发育表型均值沿地理纬度梯度的变化（Yu *et al*., 2023）。草地螟滞育诱导与解除的过程转录组分析发现 393 个基因模块与滞育关联，光周期影响组蛋白去乙酰化酶（HDAC）活性，且 HDAC 可以通过调节保幼激素影响滞育（Cui *et al*., 2022）。将亚洲玉米螟滞育期差异表达基因分为正向调控、特异表达、翻译增强和缓冲调节 4 种类型，鉴定了滞育相关的长链非编码 RNA（lncRNAs）的表达谱（Yang *et al*., 2024），进一步研究发现 H3K9me3 和 H3K27me3 表观遗传修饰在亚洲玉米螟滞育调控中发挥重要作用，H3K9me3 主要调控特定基因的转录激活，而 H3K27me3 参与转录后加工或靶基因沉默，H3K9me3 和 H3K27me3 的动态变化共同影响了滞育相关基因的表达，通过表观修饰的协同作用，实现滞育代谢调整和发育抑制（Lv *et al*., 2024）。

3.3 蛹滞育

国内昆虫蛹滞育分子调节机制的研究主要聚集于重大害虫棉铃虫滞育的调控。此外，其它如柑橘大实蝇 *Bactrocera minax*、黑纹粉蝶、菜粉蝶 *Pieirs rapae*、豆天蛾 *Clanis bilineata tsingtauica* 等滞育关联基因鉴定、比较转录组鉴定筛选到大量富集于光周期调控、内分泌激素、能量代谢、信号转导、DNA 修复、应激免疫等通路的差异表达基因（Dong *et al*., 2014, Wang *et al*., 2017; Wu *et al*., 2018; Jiang *et al*., 2021b; Zhou *et al*., 2021; Miano *et al*., 2022; Zhang *et al*., 2022a; Liao *et al*., 2024）；差异蛋白质组鉴定出滞育与磷酸化、几丁质合成、H_2O_2 与自由基降解、自噬、蛋白代谢及糖-氨基酸-脂质核心代谢通路的差异蛋白（Wang *et al*., 2020a; Li *et al*., 2025）；比较代谢组学揭示多种抗冻保护剂、氨基酸和碳水化合物等能量代谢的显著变化（Li *et al*., 2015; Wang *et al*., 2017）。

蛹滞育受 PTTH-蜕皮激素的调控，PTTH-蜕皮激素下调在棉铃虫蛹滞育中起着关键作用（Zhang *et al*., 2004b）。信息素生物合成激活神经肽（PBAN）、滞育激素（DH）能刺激前胸腺合成蜕皮激素，加速棉铃虫蛹滞育的解除（Zhang *et al*., 2004c）。棉铃虫脂肪体与大脑之间的串扰调控了发育停滞，滞育过程中基因表达受到抑制，导致血淋巴中低水平的三羧酸（Tricarboxylic acid, TCA）循环中间产物；在滞育解除时激活脂肪体，大量释放 TCA 中间产物作用于大脑刺激调节肽合成（Xu *et al*., 2012）。下调的 PTTH 和蜕皮激素降低能量代谢水平，导致脑线粒体中活性氧 ROS 积累，ROS 作为胞内信号调节棉铃虫脑中胰岛素信号路径调控滞育蛹历期延长（Zhang *et al*., 2017）。转录因子 FoxO 调节抗氧化基因的表达来降解自由基，以 ROS 作为诱发衰老的自由基，经胞内信号调节棉铃虫脑中胰岛素信号，诱导棉铃虫滞育蛹并延长历期（Zhang *et al*., 2022b）。

棉铃虫蛹滞育受多种信号通路调控。PI3K/AKT 信号抑制因子 PTEN 在棉铃虫滞育型蛹脑中表达显著降低，导致 p-AKT 水平升高。转录因子 POU 可结合 PTEN 启动子并调控其表达，POU 表达受蜕皮激素促进，但被 ROS 抑制，POU/PTEN 在响应 ROS 信号并调控 p-AKT 水平来共同调控棉铃虫蛹滞育（Song *et al*., 2018）。ROS 作为信号分子调节相关信号通路的变化，调节部分重要的基因或转录因子，如 FoxO 可调节抗氧化基因的表达来降解自由基（Zhang *et al*., 2022b）。TOR 信号通路蛋白 p-S6K 通过 ROS/AKT-S6K-CREB 轴调控 HIF-1α，介导棉铃虫滞育的启动（Wang *et al*., 2020b）。线粒体呼吸链复合物 IV（COX-IV）和 6-磷酸葡萄糖脱氢酶（G6PD）在棉铃虫蛹滞育诱导和活性氧 ROS 积累中发挥关键作用（Geng *et al*., 2021）。羰基还原酶 Cbr1 通过 ROS/Akt/CREB 途径降低棉铃虫

体内蛋白质的羰基化水平，延长蛹滞育（Geng *et al*., 2023）。低氧诱导因子（HIF-1α）在活性氧（ROS）诱导下被磷酸化，经 ROS-CK2-MKP3-p38 信号路径调节 HIF 诱导蛹滞育（Su *et al*., 2023）。棉铃虫滞育蛹脑中上调的活性氧 ROS 先活化 FoxO，再启动泛素化基因 Ubc 的表达，从而激活泛素蛋白酶体系统（Ubiquitinproteasome system, UPS），被活化的 UPS 降解，减少转化生长因子 TGFβ 发育信号，诱导脑的发育受阻，降低代谢活性，诱导蛹滞育（Zhang *et al*., 2022b）。滞育型蛹脑中 ROS 水平升高，激活 AKT，激活的 AKT 促进 Glut 表达以增强葡萄糖摄取，并抑制 GSK3β 活性，进而通过下调 Smad1 活性降低 EcR/HR3 表达，诱导蛹滞育（Song *et al*., 2023）。AMPK 通过调控棉铃虫脑中葡萄糖代谢调节蛹滞育。葡萄糖转运蛋白 1（Glut1）表达受能量感应器 AMPK 调控，AMPK 通过激活 HIF-1α 促进 Glut1 表达，后者直接结合 Glut1 启动子（Su *et al*., 2025a）。此外，AMPK 通过磷酸化抑制糖原合酶（Glycogen Synthase, GS）活性，阻止糖原合成，维持葡萄糖高水平。AMPK-HIF-1α 信号通路通过降低线粒体活性促进滞育诱导（Su *et al*., 2025b）。

基于全基因组关联分析、群体基因组学、QTL 定位、分子遗传学和细胞生物学等技术，在棉铃虫蛹滞育调节中取得系列新发现，鉴定棉铃虫滞育特性和低温适应性关联的功能基因（Jin *et al*., 2023, 2024）。环境全基因组关联分析（GWAS），在 1 号染色体上鉴定到与滞育性相关的 IGF-1 和时钟基因 *Cycle*（Jin *et al*., 2024），在 3 号和 13 号染色体上分别鉴定到了海藻糖转运蛋白编码基因 *Tret1* 和海藻糖 6-磷酸合成酶基因 *TPS*，揭示其与纬度、耐寒性显著相关（Jin *et al*., 2023）。在棉铃虫 Z 染色体上发现约 5.9 Mb 的区域与滞育性状显著关联。通过共线性比较在 1 号 Z 染色体上鉴定到 1 个倒位与 QTL1 区域重叠，用分子标记确认此倒位与滞育性状存在紧密连锁。倒位区间内共注释 214 个基因，包括 *Period*、*Clock* 和 *Cycle* 几个重要的节律通路基因。*Period* 和 *Clock* 各有 2 个非同义突变，*Cycle* 有 5 个非同义突变，突变位点影响了二聚体 PER:TIM、CYC:CLK 的结合位置和结合能力。用 CRISPR/Cas9 敲除 *Period*、*Clock* 和 *Cycle* 后，敲除品系在滞育诱导条件下表现为发育。染色体倒位抑制了重组，导致控制滞育的 3 个关键节律通路基因 *Period*、*Clock* 和 *Cycle* 共分离，形成了控制滞育的超基因抑制滞育发生（Jin *et al*., 2024）。此外，棉铃虫转录组和脂质组分析表明，脂肪体解离通过调控脂质代谢基因影响血淋巴中各类脂质的含量，进而调节棉铃虫蛹发育/滞育的抉择（Jia and Li, 2023）。

综上，光温环境信号作用于昆虫大脑，诱导上游 PTTH 激素信号和蜕皮激素下调，导致脂肪体活性下降，血淋巴中间代谢产物显著减少，导致脑细胞内线粒体的产能过程异常，诱导活性氧 ROS 积累。积累的 ROS 等细胞内信号分子，经 AMPK、胰岛素、TOR 营养信号、TGF-β 生长信号、HIF、c-Myc、JNK 等相关信号通路调控蛹滞育。转录因子 FoxO 和 HIF 等触发下游系列基因的表达，促进滞育的启动。ROS 还可以作为直接剂，氧化脑细胞中的各种蛋白质（包括酶），导致代谢活性的直接下调诱导蛹滞育。

3.4 成虫（生殖）滞育

低水平的保幼激素是诱导昆虫生殖滞育的内分泌基础，20E 对生殖滞育具有潜在调节作用，相关 JH 与 20E 的受体、转录调节因子、Micro RNA、胰岛素受体和表观遗传修饰均参与成虫生殖滞育滞育的调节。针对以成虫滞育的大猿叶虫、沙葱萤叶甲 *Galeruca daurica*、地熊蜂 *Bombus terrestris*、七星瓢虫 *Coccinella septempunctata*、日本通草蛉 *Chrysoperla nipponensis*、淡色库蚊 *Culex pipiens pallens* 等代表性种类，多组学分析筛选出大量可能与滞育相关的差异表达基因（蛋白）和 microRNA（Ma *et al*., 2019; Duan *et al*., 2021; Guo *et al*., 2021），发现能量代谢、脂肪酸代谢、细胞骨架重组、神经信号传导、内分泌激素合成与代谢等相关调控通路，鉴定差异表达蛋白（基因）主要富集于 TCA 循环、柠檬酸循环、内分泌激素生物合成与代谢、胰岛素和 mTOR 等信号调控通路（Ren *et al*., 2016; Zhang *et al*., 2019; Chen *et al*., 2021, 2023b; Liu *et al*., 2022）。

大猿叶虫在短光照下诱导发育，雌虫腹内充满卵粒，脂质积累较少；在长光照诱导生殖滞育，雌虫卵巢发育停滞，脂肪体积累大量脂肪（Liu *et al*., 2017）。保幼激素 JH 缺乏是诱导成虫生殖滞育的直接因素，通过其核受体 Met 介导滞育准备期营养代谢相关基因的表达（Liu *et al*., 2016a, 2017; Zhu *et al*., 2019b）。JH 通过受体 Met、Krüppel 同源物 Kr-h1，经 Met-Kr-h1 通路调节成虫生殖滞育（Guo *et al*., 2021; Ma *et al*., 2021a, 2021b; Hafeez *et al*., 2025），滞育异色瓢虫由于缺乏 JH，鞘翅沉积较少的类胡萝卜素，诱导生殖和滞育个体的鞘翅表型差异（Li *et al*., 2023）。从山楂叶螨 *Amphitetranychus viennensis* 筛选鉴定 6 个类胡萝卜素通路相关基因，发现沉默 *AvPD*、*AvLC/PS1* 和 *AvBCO1* 均显著降低山楂叶螨滞育率（Yang *et al*., 2025）。JH 初级应答基因 *Kr-h1* 和叉头转录因子 *FoxO* 分别是 *let-7-5p* 和 *miR-2765-3p* 两个 microRNA 的靶基因，JH 通过调控 *let-7-5p-Kr-h1* 和 *miR-2765-3p-FoxO* 反应链可调节沙葱萤叶甲的生殖滞育（Duan *et al*., 2022, 2023）。核受体家族转录因子 Seven up（*Svp*）可直接激活 JH 合成关键基因 *JHAMT1* 的表达，敲低 *Svp* 显著下调 JH 合成基因表达并降低 JH 滴度，从而调节滞育是否启动（Wang *et al*., 2025a）。组蛋白乙酰转移酶 p300/CBP 也通过保幼激素途径调控大猿叶虫的生殖滞育（An *et al*., 2025）。胰岛素信号通路调控 FoxO 转录因子调节七星瓢虫的生殖滞育（Chen *et al*., 2024）；胰岛素受体 InR1 通过胰岛素信号通路调节日本草蛉生殖滞育的启动与维持（Wang *et al*., 2025b）。

蜕皮激素（20E）作为 JH 的上游调节信号，响应滞育诱导光周期的变化，参与生殖滞育发生的调控。长光照明显抑制 20E 的产生，20E 可通过调节 JH 合成，羽化激素（ETH）可作为中间调控因子，偶联 20E 对 JH 合成的调控作用，20E-ETH-JH 信号级联通过靶向于卵巢发育和脂肪积累共同调控大猿叶虫滞育诱导（Liu *et al*., 2017; Guo *et al*., 2021），20E 的缺乏通过抑制 DNA 复制来诱导生殖滞育（Guo *et al*., 2025）。

表观遗传修饰研究可揭示昆虫如何将外部光周期信号转化为内在的激素信号，进而调控滞育。大猿叶虫夏季滞育的表观遗传调控揭示了光周期敏感的 PBAP 染色质重塑复合体通过调控组蛋白甲基化修饰影响内分泌信号，构建了“光周期-染色质重塑-钙信号-保幼激素-生殖滞育”完整的信号通路（Tian *et al*., 2025）。MYST 家族组蛋白乙酰转移酶，特别是 KAT8，通过影响 JH 信号从而调控生殖滞育的启动（An *et al*., 2024）。敲低异色瓢虫的 *Clk* 和 *cyc*（而非 per 或 tim）会干扰进入成虫生殖滞育期，表明 *Clk-cyc* 独立于 *per* 和 *tim* 调控滞育期。通过 CLK-CYC-NuA4/TIP60 复合物途径，昼夜节律蛋白与表观遗传调节剂相互作用，调控 JH 的生物合成，从而独立于昼夜节律机制调节异色瓢虫生殖滞育的诱导（Gao *et al*., 2025）。

4　总结与展望

我国 2000 年以来昆虫滞育领域的研究已从传统生理生态学系统深入至分子调控网络层面，前期研究系统揭示了环境信号感知-内分泌调控-基因表达调控网络-多种信号通路调节等方面的机制。如环境因素调节研究明确了光周期钟与光周期时间测量机制、光温协同作用、地理种群变异规律。滞育生理代谢系统阐明能量物质（海藻糖/脂类）动态转化、激素（JH/20E/DH/PTTH 等）调控及滞育关联酶调节作用。滞育的分子调节机制及多种信号通路：发现内分泌激素、生物钟基因 *Cycle* 等关键调控因子，揭示 ROS 信号、胰岛素/TGF-β 等通路在滞育调控中的枢纽作用；系统构建了滞育相关代谢通路与表观遗传调控网络框架。后基因组时代基于多组学联合基因编辑等分子生物学技术对滞育调控网络的探索为深入理解昆虫滞育、乃至生命发育可塑性机制提供了新视角，为开发与利用分子靶标操控滞育发展害虫控制技术提供新思路，为害虫防治和有益昆虫利用提供新方法。未来昆虫滞育的研究建议进一步拓展以下两个方面：

一方面，基础理论研究深入揭示滞育系统的

调节机制。将研究视角从单一物种、特定实验种群、独特滞育虫态、单个或少数功能基因与代谢/信号通路向多因素交互效应（多重环境信号整合识别-滞育适应性表型-表观遗传与进化）延伸。针对非模式昆虫滞育的特异性、复杂性和多样性，开展多维度、跨层级、全周期的滞育表型调控与功能研究，揭示昆虫不同滞育类型的共性调节机制，揭示非模式昆虫季节性适应分子进化调控的普适性规律。为预测全球气候变化下昆虫种群动态提供理论基础。

另一方面，结合滞育生物学，重视应用技术拓展与实践。滞育诱导-维持-解除-滞育后发育启动转换过程的动态调控机制，特别是传粉昆虫、天敌昆虫、重大害虫突出多尺度整合与全球气候变化背景下滞育种群监测、种群调节及其应用。当前滞育调控研究多基于室内可控条件，缺乏自然动态变化环境条件重大害虫、传粉与天敌昆虫滞育种群动态的长期系统观测。滞育调控在实践上如何调节寄主植物受害敏感期与害虫种群暴发期异步、传粉昆虫发生与靶标授粉作物花期同步、天敌种群发生与害虫种群高峰同步等物候学调节机制值得系统研究与实践。推动滞育理论成果向昆虫管理科学实践应用的转化，开发基于害虫滞育调控特异靶标的精准控制策略、人工合成滞育诱导剂或抑制剂，发展基于滞育调控的传粉与天敌昆虫人工繁育种群复壮技术。

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