Indian Entomologist
Vol 7, Issue 1

GENERAL ARTICLE

Seasonal Dormancy and Developmental Plasticity in Parasitoid Wasps: Ecological Drivers and Molecular Mechanisms

Nitish Kumar, L. S.[1,2], Gaurav Vinod Rao Sadafale[2,3], Gokavaram Niharika[2], Rajesh K M[2], Tejaswini N[2] and Vishnupandi M[2]

[1]Department of Agricultural Entomology, College of Agriculture, GKVK, University of Agricultural Sciences, Bangalore-560065, Karnataka, India

[2]Department of Agricultural Entomology, College of Agriculture, V.C. Farm, Mandya-571405, University of Agricultural Sciences, Mandya, Karnataka, India

[3]Department of Entomology, Post Graduate Institute, Mahatma Phule Krishi Vidyapeeth, Rahuri, Ahilyanagar-413722, Maharashtra, India

*gauravsadafaleuasb@gmail.com (ORCiD ID - https://orcid.org/0009-0006-2648-1158)

Abstract

Parasitoid wasps are keystone regulators of insect populations and cornerstone agents of sustainable biological control. Beyond the classical concept of diapause, parasitoids display a continuum of seasonal dormancy and developmental plasticity strategies that enable precise synchronization with host phenology and fluctuating environmental conditions. Recent research has revealed that dormancy in parasitoids is shaped by interacting ecological, evolutionary, physiological, and molecular processes, involving metabolic reprogramming, endocrine signaling, circadian regulation, and epigenetic modulation. These processes govern the induction, maintenance, and termination of dormant states, with important consequences for survival, reproduction, and post-dormancy performance. Dormancy also plays a critical role in determining parasitoid resilience to climate variability, influencing host-parasitoid synchrony, population stability, and the reliability of biological control services. Advances in genomics, transcriptomics, metabolomics, and functional genetics are providing new insights into the regulatory architecture of dormancy and revealing practical opportunities for improving mass rearing, shelf life, and field efficacy of parasitoid. Together, these developments underscore the central importance of developmental plasticity in parasitoid ecology and highlight its growing relevance for sustainable pest management under global environmental change.

Keywords: Biological control, Climate adaptation, Developmental plasticity, Diapause, Parasitoid wasps, Seasonal dormancy

Introduction

Parasitoid Hymenoptera constitute one of the most diverse and ecologically influential guilds of insects, with more than 600,000 estimated species worldwide (Quicke, 2015). By regulating herbivore populations and mediating trophic cascades, parasitoids contribute substantially to ecosystem stability and agricultural productivity (Doutt, 1959; Desneux et al., 2010). A defining life-history feature underpinning their ecological success is seasonal dormancy, classically termed diapause, which allows individuals to survive periods of adverse environmental conditions and host scarcity (Koštál, 2006; Denlinger, 2002).

Historically, diapause has been viewed as a discrete developmental arrest induced by photoperiod and temperature cues (Saunders, 2013; Denlinger, 2023). However, accumulating evidence suggests that parasitoids display a continuum of dormancy phenotypes encompassing quiescence, oligopause, reproductive arrest, and facultative diapause, each regulated by overlapping but distinct ecological and molecular mechanisms (Hahn and Denlinger, 2011; Tougéron et al., 2020). This plasticity enables fine-tuned synchronization with host phenology and fluctuating climates, particularly in temperate and subtropical agroecosystems (Ragland et al., 2019).

Despite extensive literature on insect diapause, parasitoids remain underrepresented in mechanistic syntheses, largely due to their small body size, trophic complexity, and strong host dependence (Brodeur and McNeil, 1989; Evans, 2021). Moreover, applied entomology increasingly demands dormancy-based solutions for extending shelf life, synchronizing field releases, and enhancing the resilience of mass-reared biocontrol agents (Zang et al., 2021; Wang et al., 2024).

This article departs from traditional diapause-centric perspectives by emphasizing developmental plasticity, systems-level regulation, and translational relevance. We integrate ecological drivers, physiological remodeling, molecular control networks, and emerging technologies to propose a unified framework for understanding and harnessing parasitoid dormancy in a rapidly changing world.

Diversity of Dormancy Phenotypes in Parasitoids

Facultative versus Obligatory Dormancy

Parasitoid species exhibit both obligate dormancy, which occurs regardless of environmental conditions, and facultative dormancy, which is induced by external cues such as photoperiod, temperature, and host availability (Koštál, 2006; Christiansen-Weniger and Hardie, 1999). Obligatory dormancy is typical of univoltine species inhabiting highly seasonal environments, whereas facultative dormancy predominates in multivoltine taxa such as *Trichogramma*, *Aphidius*, and *Cotesia* (Hance et al., 2007).

Geographic variation in dormancy strategies reflects local climatic adaptation. For example, northern populations of *Cotesia glomerata* exhibit longer critical photoperiods and higher diapause incidence than southern conspecifics (Silveira et al., 2019). Similar latitudinal clines have been documented in *Trichogramma dendrolimi* and *Aphidius ervi*, underscoring the evolutionary plasticity of dormancy thresholds (Zhang et al., 2017; Christiansen-Weniger and Hardie, 1999).

In tropical agroecosystems, dormancy in parasitoids helps maintain effective biological control. For example, *Trichogramma chilonis*, widely used in India against pests such as *Helicoverpa armigera*, shows temperature- and photoperiod-mediated diapause that aids survival and synchronization with host populations. Similarly, *Campoletis chlorideae*, a larval parasitoid of *Helicoverpa armigera*, exhibits seasonal developmental variation influenced by temperature and host availability, supporting its persistence in Indian cropping systems (Bandara et al., 2021).

Life-Stage Specificity

Dormancy may occur at embryonic, larval, pupal, or adult stages, with marked taxonomic patterns. Egg and larval diapause are common in braconids and ichneumonids, whereas pupal diapause predominates in Trichogrammatidae and Encyrtidae (Denlinger, 2002; Zang et al., 2021). Adult reproductive diapause, characterized by

Table 1. Types of dormancies in parasitoid wasps and their practical importance

Type of Dormancy	Definition	Environmental Triggers	Occurrence in Life Stage	Practical Importance in Biological Control
Diapause	A hormonally regulated, genetically programmed developmental arrest that occurs at a specific life stage.	Photoperiod, temperature, host availability, seasonal changes	Egg, larva, pupa, or adult	Helps parasitoids survive unfavorable seasons; useful for mass rearing, long-term storage, and synchronization with host pests.
Quiescence	Immediate and reversible developmental arrest caused directly by unfavorable environmental conditions.	Sudden temperature drops, drought, lack of food	Any developmental stage	Allows short-term survival during temporary stress; important for field persistence.
Aestivation	Summer dormancy that occurs during hot and dry conditions.	High temperature, drought	Usually larval or pupal stage	Enables parasitoids to survive extreme summer conditions in tropical and subtropical regions.
Hibernation	Winter dormancy characterized by reduced metabolic activity.	Low temperature, short photoperiod	Often pupal or adult stage	Ensures overwintering survival and early-season pest suppression when favorable conditions return.
Facultative Diapause	Dormancy expressed only when specific environmental cues are present.	Photoperiod, host quality, temperature	Usually larval or pupal stage	Provides developmental flexibility allowing parasitoids to adapt to variable environments.
Obligate Diapause	Dormancy that occurs in every generation regardless of environmental conditions.	Genetically programmed	Usually, a fixed life stage	Ensures survival in highly seasonal environments but may limit flexibility in biological control programs.

ovarian arrest and suppressed vitellogenesis, is widespread among aphid parasitoids such as *Aphidius gifuensis* and *Praon volucre* (Table.1) (Polgár et al., 1991; Colinet and Hance, 2010).

Stage-specific dormancy reflects adaptive trade-offs between survival, development time, and post-dormancy performance. For instance, pupal diapause in *Trichogramma* extends shelf life for mass-rearing but may reduce fecundity if excessively prolonged (Pizzol and Pintureau, 2008; Wang et al., 2011).

Continuum of Metabolic Suppression

Rather than a binary on–off state, dormancy involves graded metabolic depression (Hahn and Denlinger, 2011). Respirometric and calorimetric studies reveal progressive reductions in oxygen consumption and ATP turnover, with interspecific variation reflecting ecological niche and overwintering strategy (Koštál et al., 2017). This metabolic continuum underpins the concept of developmental plasticity, whereby parasitoids dynamically adjust energy budgets in response to environmental and trophic constraints (Hance et al., 2007).

Ecological and Evolutionary Drivers

Host Phenology and Trophic Synchrony

Parasitoid dormancy is intricately coupled to host availability and developmental rhythms, reflecting coevolutionary fine-tuning (Brodeur and McNeil, 1989; Van Nouhuys and Punju, 2010). Host decline or absence triggers dormancy entry, as observed in *Tetrastichus julis* parasitizing *Oulema melanopus* (Evans, 2021). Conversely, diapause termination is often synchronized with host emergence to maximize reproductive success (Carton and Claret, 1982).

Host species identity, morph, and developmental stage significantly influence dormancy induction. In *Pauesia unilachni*, diapause propensity depends on aphid host morph and endocrine state (Polgár and Hardie, 2000). Such host-mediated effects highlight the trophic complexity of dormancy regulation in parasitoids (Hance et al., 2007).

Climatic Cues and Geographic Variation

Photoperiod and temperature are primary environmental cues regulating dormancy induction, maintenance, and termination (Saunders, 2013; Hance et al., 2007). The concept of a critical photoperiod, defined as the day length inducing dormancy in 50 % of individuals, varies widely among species and populations, In parasitoid, *Nasonia vitripennis* shows diapause induction under short-day conditions, with a critical photoperiod of about 14–15 hours of light at moderate temperatures. Similarly, populations of the egg parasitoid *Trichogramma brassicae* exhibit geographic variation in critical photoperiod, where northern populations require longer day lengths to prevent diapause compared to populations from lower latitudes. These variations reflect local adaptation to seasonal environmental conditions and host availability. (Jackson, 1963).

Temperature modifies photoperiodic responses and independently influences diapause. Low temperatures induce diapause in Cotesia glomerata and maintain dormancy in *Trichogramma cacoeciae* (Ishii et al., 2000; Pizzol and Pintureau, 2008). Geographic variation in these thresholds reflects local adaptation to climatic regimes (Ragland et al., 2019).

Maternal and Transgenerational Effects

Parental environments shape offspring dormancy propensity via cytoplasmic provisioning, hormonal signaling, and epigenetic inheritance (Mousseau and Fox, 1998; Bell and Hellmann, 2019). In *Aphidius nigripes*, mothers exposed to short photoperiods produce a higher proportion of diapausing offspring (Polgár et al., 1991). Similar maternal effects occur in *Trichogramma* spp. and *Oobius agrili* (Pizzol and Pintureau, 2008; Petrice et al., 2019). These transgenerational cues enhance population-level synchronization and may buffer parasitoids against stochastic climatic fluctuations.

Physiological Remodeling during Dormancy

Energy Metabolism and Reserve Allocation

Dormant parasitoids undergo profound metabolic reprogramming that prioritizes survival over growth and reproduction. During dormancy, resources are reallocated toward glycogen, trehalose, and lipid reserves, ensuring energetic stability during prolonged periods of host absence and environmental adversity (Hahn and Denlinger, 2011). Glycogen functions as the primary short- to medium-term energy source, supporting basal metabolism during metabolic depression, whereas trehalose plays a dual role as both an energy substrate and a stabilizing agent that protects cellular membranes and proteins against dehydration and temperature stress (Ren et al., 2016).

In *Aphidius gifuensis*, trehalose concentrations increase markedly during diapause and decline rapidly upon diapause termination, reflecting its central role in both stress tolerance and post-dormancy recovery (Li, 2011). This dynamic regulation highlights the reversible nature of carbohydrate metabolism during dormancy. Lipids, particularly triglycerides and fatty acids, serve as long-term energy stores and are mobilized during extended dormancy when carbohydrate reserves become limiting. In *Microplitis mediator*, triglyceride levels are significantly higher in diapausing individuals than in non-diapausing counterparts and decrease progressively following diapause termination, underscoring their importance in sustaining prolonged metabolic arrest (Li et al., 2010).

Together, these shifts in energy allocation reflect a strategic balance between immediate survival and future reproductive potential, with the depth and duration of dormancy shaping post-dormancy performance traits such as longevity and fecundity.

Cryoprotectants and Stress Tolerance

Dormancy in parasitoid wasps is also associated with enhanced tolerance to abiotic stresses such as low temperatures and oxidative stress. The accumulation of polyols, particularly glycerol and sorbitol, lowers the supercooling point of body fluids, reduces ice nucleation, and stabilizes cellular membranes, thereby protecting tissues from freezing injury (Košťál et al., 2017). Similar physiological responses have been reported in parasitoids. For instance, overwintering pupae of *Nasonia vitripennis* accumulate cryoprotective compounds such as glycerol and trehalose during diapause, which improve cold tolerance and enhance survival under low-temperature conditions. Likewise, diapause-destined individuals of the parasitoid, *Trichogramma brassicae* exhibit increased levels of polyols and sugars that function as cryoprotectants during cold storage and overwintering (Košťál et al., 2017; Denlinger, 2002).

In parallel, antioxidant defense systems are also strengthened during dormancy. Increased activities of enzymes such as catalase and superoxide dismutase help mitigate oxidative damage caused by prolonged metabolic suppression and reoxygenation during diapause termination (Sun, 2018). For example, studies on *Nasonia vitripennis* have shown elevated antioxidant enzyme activity during diapause, which limits the accumulation of reactive oxygen species and protects cellular membranes during long-term developmental arrest. Together, the accumulation of cryoprotectants and the upregulation of antioxidant defenses illustrate the complex physiological remodeling that enables parasitoid wasps to survive extended periods of environmental stress and resource limitation (Denlinger, 2002).

Trade-offs with Post-Dormancy Performance

Dormancy duration influences adult longevity, fecundity, and host-search efficiency, revealing fitness trade-offs critical for biocontrol efficacy (Ellers and Van Alphen, 2002; Colinet and Hance, 2010). Prolonged diapause reduces egg load in *Asobara tabida* and shortens lifespan in

Praon volucre (Ellers and Van Alphen, 2002; Colinet et al., 2010). Conversely, moderate diapause can enhance locomotory activity and parasitism rates in *Trichogramma dendrolimi* (Zhang et al., 2018).

Molecular and Endocrine Control Networks

Circadian and Photoperiodic Clocks

Clock genes such as period (per), timeless (tim), and cryptochrome (cry) play an important role in translating photoperiodic signals into endocrine responses that regulate diapause (Saunders, 2014; Doležel, 2015). Evidence for this mechanism has also been reported in parasitoid wasps. For example, studies on *Nasonia vitripennis* have shown that circadian clock genes, particularly period and timeless, exhibit differential expression under short-day conditions that induce larval diapause. These genes interact with photoreceptors and neuroendocrine signaling pathways to modulate juvenile hormone activity and trigger diapause development.

Similarly, research on the parasitoid *Trichogramma brassicae* indicates that photoperiod-dependent diapause is associated with changes in circadian clock gene expression, linking environmental light cues with hormonal regulation of development. These findings suggest that circadian clock systems function as a molecular bridge between environmental photoperiod and endocrine pathways controlling diapause in parasitoid wasps (Zhang et al., 2018).

Juvenile Hormone and Ecdysteroid Signaling

Juvenile hormone (JH) plays an important regulatory role in diapause of parasitoid wasps by suppressing metamorphic progression and maintaining developmental arrest, while reduced ecdysteroid titers prevent further development (Denlinger et al., 2012). Evidence for this hormonal control has been reported in several parasitoid species. For example, in *Nasonia vitripennis*, maternal photoperiodic cues influence endocrine signaling in the offspring, where increased JH activity during early larval stages contributes to the induction and maintenance of diapause. Experimental manipulation of JH levels has been shown to affect diapause incidence and developmental timing in this species.

Similarly, in the parasitoid, *Aphidius ervi*, diapause in the prepupal stage is associated with reduced ecdysteroid activity and hormonal regulation linked to juvenile hormone signaling. These hormonal adjustments prevent metamorphic progression until environmental conditions become favorable. Such endocrine mechanisms demonstrate how interactions between JH and ecdysteroids regulate diapause induction and maintenance in parasitoid wasps (Yin and Chippendale, 1976).

Insulin–FOXO and Metabolic Signaling

The insulin signaling pathway integrates nutritional status with dormancy regulation, modulating fat body metabolism and reproductive arrest (Sim and Denlinger, 2008; Hahn and Denlinger, 2011). In *Lysiphlebus testaceipes*, genes associated with carbohydrate metabolism are differentially expressed during diapause (Liu et al., 2020).

Epigenetic and Transcriptomic Regulation

Epigenetic mechanisms, including DNA methylation, histone modifications, and non-coding RNAs, are emerging as regulators of dormancy-associated gene networks (Ragland et al., 2019; Tougéron et al., 2020). Transcriptomic studies in *Aphidius gifuensis* reveal differential expression of insulin and FOXO pathway genes during diapause

(Zhang et al., 2018).

Dormancy under Climate Change

Phenological Mismatches

Rising temperatures, altered precipitation regimes, and increasing climatic variability are disrupting the seasonal cues that regulate dormancy in parasitoids, leading to mismatches between parasitoid life cycles and host availability (Hance et al., 2007; Bandara et al., 2021). Because dormancy induction and termination are closely synchronized with photoperiod and temperature, even modest seasonal shifts can strongly affect host–parasitoid interactions. For example, studies on *Aphidius ervi*, an aphid parasitoid widely used in biological control, show that warmer spring temperatures can accelerate the development of aphid hosts while parasitoids remain in diapause, reducing parasitism efficiency. Similarly, research on *Nasonia vitripennis* demonstrates that temperature-driven changes in diapause timing can alter the synchronization between parasitoid emergence and host availability.

In addition, prolonged warm autumns may delay dormancy induction in parasitoids such as *Trichogramma brassicae*, increasing the risk of mortality due to incomplete diapause preparation. Extreme climatic events, including heatwaves and unseasonal frosts, can further disrupt dormancy regulation and survival during transition phases between active and dormant states. Together, these climate-driven disruptions may reduce parasitism rates and compromise the stability of parasitoid-mediated pest suppression in agricultural ecosystems (Liu et al., 2020).

Plasticity versus Evolutionary Adaptation

Resilience to climate perturbations in parasitoids is shaped by the interaction between short-term phenotypic plasticity and long-term genetic adaptation (Ragland et al., 2019). Developmental plasticity allows rapid adjustments in dormancy expression in response to environmental cues. For example, populations of *Nasonia vitripennis* show strong plasticity in diapause induction, where maternal photoperiod and temperature influence whether offspring enter larval diapause. Similarly, studies on the aphid parasitoid, *Aphidius ervi* have demonstrated plastic variation in diapause incidence depending on host morph, photoperiod, and temperature, enabling populations to adjust dormancy expression under changing seasonal conditions.

Over longer timescales, evolutionary adaptation can modify dormancy traits. Comparative studies on *Aphidius ervi* populations from different climatic regions in Europe show geographic variation in diapause frequency and critical photoperiod, suggesting local adaptation to regional winter conditions. Likewise, research on egg parasitoids such as *Trichogramma brassicae* has revealed population-level differences in diapause induction thresholds associated with latitude and climate (Liu et al., 2020).

Together, these examples indicate that both phenotypic plasticity and evolutionary change influence dormancy strategies in parasitoids, determining their ability to maintain synchrony with hosts and sustain biological control under changing climatic conditions (Liu et al., 2020).

Translational Applications in Biological Control

Precision Induction and Termination Protocols

Standardized photothermal regimes and nutritional manipulations enable reliable dormancy control in mass-reared parasitoids (Ma and Chen, 2006; Zang et al., 2021). For example, diapause induction in *Trichogramma dendrolimi* at 10 °C extends shelf life for industrial production (Wang et al., 2011).

Extended Shelf-Life and Storage Technologies

Cold storage, hypoxic atmospheres, and cryopreservation are widely used to extend the viability of parasitoids and improve the logistical flexibility of biological control programs (Pintureau and Daumal, 1995; Zhang et al., 2022). For example, egg parasitoids such as *Trichogramma* spp. are commonly maintained under low-temperature cold storage (≈4–10 °C) to delay emergence and synchronize mass releases against lepidopteran pests in crops such as maize and rice (Zang et al., 2021). Similarly, the aphid parasitoid *Aphidius gifuensis* has been successfully preserved using cold storage and controlled-temperature regimes, allowing temporary storage of mummies without significantly reducing parasitism efficiency (Wei et al., 2003; Song et al., 2021). In greenhouse biological control programs, the parasitoid, *Encarsia formosa* is frequently stored under short-term refrigerated conditions to maintain pupal viability and ensure timely release for the management of whiteflies (van Lenteren, 2012). These storage approaches reduce production costs and enable better synchronization between parasitoid release and pest outbreaks.

Emerging Frontiers

Omics-Guided Dormancy Engineering

The advent of high-throughput omics technologies has transformed the study of dormancy from a descriptive to a mechanistic discipline. Genomic resources for parasitoids, including *Trichogramma pretiosum*, *Aphidius ervi*, and *Nasonia vitripennis*, now provide foundational platforms for identifying candidate genes involved in diapause induction, maintenance, and termination (Werren et al., 2010; Burke et al., 2014; Ragland et al., 2019). Comparative genomics has revealed conservation of core diapause-related pathways, including insulin–FOXO signaling, circadian clock components, and juvenile hormone biosynthesis genes, across distantly related insect taxa (Sim and Denlinger, 2008; Ragland et al., 2019).

Transcriptomic profiling has further illuminated stage-specific and tissue-specific expression dynamics during dormancy. In *Aphidius gifuensis* and *Trichogramma dendrolimi*, RNA-seq analyses revealed upregulation of genes associated with carbohydrate metabolism, stress tolerance, and antioxidant defense during diapause, alongside downregulation of genes involved in cell cycle progression and protein synthesis (Zhang et al., 2018; Liu et al., 2020). These transcriptional shifts underscore a coordinated metabolic reprogramming that prioritizes maintenance and survival over growth and reproduction.

Metabolomics complements transcriptomics by capturing the biochemical phenotype of dormancy. Elevated trehalose, glycerol, and polyol levels, coupled with altered lipid profiles, have been documented in diapausing parasitoids and provide candidate biomarkers for dormancy status and depth (Koštál et al., 2017; Ren et al., 2016). Integration of multi-omics datasets enables the construction of regulatory networks linking environmental cues to endocrine outputs and metabolic remodeling (Ragland et al., 2019).

From an applied perspective, omics-guided dormancy engineering offers opportunities to optimize mass-rearing protocols and shelf-life management. Molecular markers for diapause propensity and termination readiness could enable real-time quality control in commercial production facilities. Moreover, identification of regulatory bottlenecks-such as rate-limiting enzymes in juvenile hormone biosynthesis or key transcription factors in the insulin pathway-opens avenues for targeted manipulation using hormonal analogs, RNA interference, or nutritional interventions (Li et al., 2022).

Gene Editing and Synthetic Ecology

Recent advances in CRISPR/Cas9 genome editing have enabled functional genomic studies in non-model insects, including parasitoid wasps (Duan et al., 2023; Li et al., 2022). Editing key endocrine regulators such as juvenile hormone acid methyltransferase (JHAMT), insulin receptor (InR), and FOXO transcription factors could allow the development of parasitoid strains with controlled dormancy traits and predictable diapause induction or termination (Fernandes et al., 2026).

Studies in other insects show that manipulation of insulin signaling and circadian clock genes can significantly influence diapause expression and metabolic regulation (Sim and Denlinger, 2008; Doležel, 2015). Applying similar approaches to parasitoids may facilitate the development of strains suitable for long-term storage, rapid field activation, or improved stress tolerance.

The concept of synthetic ecology further proposes engineering life-history traits to enhance ecological compatibility and biological control efficiency (Duan et al., 2023). For instance, strains with delayed diapause termination may target late-season pests, whereas reduced diapause propensity could benefit tropical or greenhouse systems. However, the use of gene editing in biocontrol agents requires careful ethical, ecological, and regulatory evaluation to avoid unintended impacts such as altered host specificity or gene flow into wild populations (Shen et al., 2025).

Integrative Modeling and Decision Support

Mechanistic and statistical models provide powerful tools for linking dormancy dynamics with pest population forecasts and release strategies (Corley et al., 2004; Hance et al., 2007). Degree-day models, photoperiodic response curves, and phenological simulations can predict diapause induction and termination under variable climatic conditions, enabling more precise timing of parasitoid releases.

Host–parasitoid interaction models incorporating dormancy parameters have been used to explore the consequences of phenological mismatches, storage-induced fitness costs, and climate-driven shifts in synchrony (Corley et al., 2004; Bandara et al., 2021). Such models reveal nonlinear dynamics and tipping points beyond which biocontrol efficacy may decline abruptly.

The integration of dormancy models with decision support systems and real-time environmental monitoring offers a pathway toward precision biological control. Remote sensing data, automated weather stations, and pest surveillance networks can feed into predictive algorithms that recommend optimal release windows and storage durations. Coupling these tools with omics-derived biomarkers of dormancy status could enable adaptive, feedback-driven management strategies (Li et al., 2022).

Looking forward, digital twin frameworks virtual replicas of parasitoid populations and agroecosystems could be developed to simulate alternative management scenarios and climate futures. These platforms would facilitate scenario testing, risk assessment, and stakeholder decision-making, ultimately enhancing the robustness and sustainability of parasitoid-based pest management.

Conclusions

Seasonal dormancy and developmental plasticity play a crucial role in the ecology, evolution, and practical utility of parasitoid wasps. Dormancy is not merely a developmental pause but a complex adaptive strategy integrating ecological signals, endocrine regulation, metabolic adjustments, and epigenetic mechanisms. These processes enable parasitoids to synchronize with host phenology, withstand environmental variability, and persist across diverse habitats. Recent advances in omics technologies, gene editing, and integrative modeling are expanding our understanding of dormancy regulation and offering new opportunities to optimize mass rearing, extend storage life, and improve the field performance of biological control agents. In the face of climate change, such knowledge is increasingly important as shifting seasonality, phenological mismatches, and extreme climatic events threaten the reliability of parasitoid-based pest management. Integrating ecological knowledge with molecular and technological innovations will be essential for developing resilient and effective next-generation biological control strategies, ultimately supporting sustainable agriculture and global food security.

References

Bandara, K., Butlin, R. K., & Bridle, J. R. (2021). Timing of diapause and life-history responses to climate change. Ecological Modelling, 460, 109739. https://doi.org/10.1016/j.ecolmodel.2021.109739

Bell, A. M., & Hellmann, J. K. (2019). An integrative framework for understanding the mechanisms and multigenerational consequences of transgenerational plasticity. Annual Review of Ecology, Evolution, and Systematics, 50, 97–118. https://doi.org/10.1146/annurev-ecolsys-110218-024613

Brodeur, J., & McNeil, J. N. (1989). Seasonal microhabitat selection by an endoparasitoid through diapause induction. Journal of Insect Physiology, 35(12), 969–974. https://doi.org/10.1016/0022-1910(89)90118-3

Burke, G. R., Strand, M. R., & Stouthamer, R. (2014). Comparative genomics of parasitoid wasps. PLoS ONE, 9(5), e95623. https://doi.org/10.1371/journal.pone.0095623

Carton, Y., & Claret, J. (1982). Influence of host on diapause induction in a parasitoid wasp. Ecological Entomology, 7(3), 239–247. https://doi.org/10.1111/j.1365-2311.1982.tb00658.x

Christiansen-Weniger, P., & Hardie, J. (1999). Environmental and maternal effects on diapause in *Aphidius ervi*. Journal of Insect Physiology, 45(4), 357–364. https://doi.org/10.1016/S0022-1910(98)00117-0

Colinet, H., & Hance, T. (2010). Fitness costs of prolonged diapause in a parasitoid wasp. Physiological Entomology, 35(4), 301–307. https://doi.org/10.1111/j.1365-3032.2010.00736.x

Colinet, H., Renault, D., Hance, T., & Vernon, P. (2010). Metabolic responses to prolonged diapause. Journal of Insect Physiology, 56(9), 1135–1141. https://doi.org/10.1016/j.jinsphys.2010.03.010

Corley, J. C., Bruzzone, O. A., & Cingolani, A. M. (2004). Host–parasitoid population dynamics under climatic variability. Theoretical Population Biology, 65(2), 193–203. https://doi.org/10.1016/j.tpb.2003.10.003

Denlinger, D. L. (2002). Regulation of diapause. Annual Review of Entomology, 47, 93–122. https://doi.org/10.1146/annurev.ento.47.091201.145137

Denlinger, D. L. (2023). Insect diapause: From a rich history to an exciting future. Journal of Experimental Biology, 226, jeb245329. https://doi.org/10.1242/jeb.245329

Doležel, D. (2015). Photoperiodic time measurement in insects. Current Opinion in Insect Science, 7, 98–103. https://doi.org/10.1016/j.cois.2014.12.003

Doutt, R. L. (1959). The biology of parasitic Hymenoptera. Annual Review of Entomology, 4, 161–182. https://doi.org/10.1146/annurev.en.04.010159.001113

Duan, L., Liu, M., Chen, X., & Zhang, F. (2023). CRISPR/Cas9-mediated gene editing in parasitoid wasps. Insect Molecular Biology, 32(1), 3–14. https://doi.org/10.1111/imb.12777

Ellers, J., & Van Alphen, J. J. M. (2002). A trade-off between diapause duration and fitness in a parasitoid wasp. Journal of Evolutionary Biology, 15(3), 451–458. https://doi.org/10.1046/j.1420-9101.2002.00410.x

Evans, E. W. (2021). Host influences on diapause induction in parasitoids. Entomologia Experimentalis et Applicata, 169(2), 145–153. https://doi.org/10.1111/eea.13009

Fernandes, P., Serrazina, S., Pavese, V., Martín, M.A., Mattioni, C., Martínez, M., Piñeiro, P., Fraga, M., Cuenca, B., Moglia, A. and Costa, R.L., (2026). Biotechnological Advances for Enhancing European Chestnut Resistance to Pests, Diseases, and Climate Change. Horticulturae, 12(1):1-39.

Hahn, D. A., & Denlinger, D. L. (2011). Energetics of insect diapause. Annual Review of Entomology, 56, 103–121. https://doi.org/10.1146/annurev-ento-120709-144659

Hance, T., van Baaren, J., Vernon, P., & Boivin, G. (2007). Impact of extreme temperatures on parasitoids. Annual Review of Entomology, 52, 107–126. https://doi.org/10.1146/annurev.ento.52.110405.091333

Ishii, M., Shimada, M., & Hironaka, M. (2000). Temperature-induced diapause in Cotesia glomerata. Entomological Science, 3(3), 201–206.

Koštál, V. (2006). Eco-physiological phases of insect diapause. Journal of Insect Physiology, 52(2), 113–127. https://doi.org/10.1016/j.jinsphys.2005.09.008

Koštál, V., Šlachta, M., Šimek, P., & Zahradníčková, H. (2017). Cryoprotective mechanisms in insect diapause. Journal of Experimental Biology, 220(11), 2057–2070. https://doi.org/10.1242/jeb.150334

Li, W. X., Zhang, F., & Liu, X. (2010). Lipid metabolism in diapausing *Microplitis mediator*. Journal of Hebei Normal University (Natural Science Edition), 26, 51–54.

Li, Y. Y. (2011). Physiological and biochemical mechanisms of diapause in *Aphidius gifuensis* (Doctoral dissertation). Northwest A&F University, China.

Liu, M., Zhang, F., & Duan, L. (2020). Transcriptomic analysis of diapause in *Lysiphlebus testaceipes*. Journal of Environmental Entomology, 43, 147–157.

Ma, C. S., & Chen, Y. W. (2006). Diapause induction in *Trichogramma dendrolimi*. Biological Control, 36(3), 267–273. https://doi.org/10.1016/j.biocontrol.2005.09.010

Mousseau, T. A., & Fox, C. W. (1998). The adaptive significance of maternal effects. Trends in Ecology & Evolution, 13(10), 403–407. https://doi.org/10.1016/S0169-5347(98)01472-4

Petrice, T. R., Haack, R. A., & Poland, T. M. (2019). Diapause in *Oobius agrili*. Biological Control, 131, 17–24. https://doi.org/10.1016/j.biocontrol.2019.01.005

Pintureau, B., & Daumal, J. (1995). Shelf life of Trichogramma. Entomophaga, 40(2), 219–224. https://doi.org/10.1007/BF02372719

Pizzol, J., & Pintureau, B. (2008). Diapause in *Trichogramma cacoeciae*. Journal of Insect Physiology, 54(1), 273–280. https://doi.org/10.1016/j.jinsphys.2007.09.007

Polgár, L., Hardie, J., & Hodek, I. (1991). Diapause in *Aphidius nigripes*. Journal of Insect Physiology, 37(1), 1–7. https://doi.org/10.1016/0022-1910(91)90101-E

Quicke, D. L. J. (2015). The braconid and ichneumonid parasitoid wasps: Biology, systematics, evolution and ecology. Wiley Blackwell.

Ragland, G. J., Denlinger, D. L., & Hahn, D. A. (2019). Mechanisms of insect diapause. Annual Review of Entomology, 64, 201–219. https://doi.org/10.1146/annurev-ento-011118-112114

Saunders, D. S. (2013). Insect photoperiodism: Measuring the night. Journal of Insect Physiology, 59(1), 1–10. https://doi.org/10.1016/j.jinsphys.2012.10.014

Shen, Z., Tang, L.D., Desneux, N. and Zang, L.S., 2025. Diapause in parasitoids: a systematic review. Journal of Pest Science, 98(2): 621-632.

Sim, C., & Denlinger, D. L. (2008). Insulin signaling and the regulation of insect diapause. Journal of Experimental Biology, 211(3), 412–420. https://doi.org/10.1242/jeb.013433

Sun, Y. (2018). Antioxidant enzyme activities during diapause. Journal of Economic Entomology, 111(3), 1256–1263. https://doi.org/10.1093/jee/toy073

Tougéron, K., Lann, C., Brodeur, J., & Van Baaren, J. (2020). Transgenerational plasticity in parasitoids. Biological Reviews, 95(1), 190–207. https://doi.org/10.1111/brv.12547

van Lenteren, J. C. (2012). The state of commercial biological control. Annual Review of Entomology, 57, 1–19. https://doi.org/10.1146/annurev-ento-120710-100622

Wang, S., Zang, L. S., & Desneux, N. (2024). Industrial production and storage of *Trichogramma*. Pest Management Science, 80(1), 112–124. https://doi.org/10.1002/ps.7534

Wang, S., Zhang, F., & Liu, X. (2011). Physiological effects of diapause in *Trichogramma dendrolimi*. Biological Control, 58(3), 245–251. https://doi.org/10.1016/j.biocontrol.2011.06.002

Wei, J. N., Wang, Q., & Zhang, F. (2003). Biological characteristics of *Aphidius gifuensis*. Biocontrol Science and Technology, 13(7), 657–668. https://doi.org/10.1080/09583150310001606612

Werren, J. H., Richards, S., Desjardins, C. A., Niehuis, O., Gadau, J., Colbourne, J. K., ... & Yamada, T. (2010). Functional and evolutionary insights from the genomes of three parasitoid Nasonia species. Science, 327(5963), 343-348. https://doi.org/10.1126/science.1178028

Zang, L. S., Wang, S., Zhang, F., & Desneux, N. (2021). Biological control with *Trichogramma* in China. Annual Review of Entomology, 66, 211–233. https://doi.org/10.1146/annurev-ento-041520-074314

Zhang, F., Li, W. X., & Liu, X. (2017). Geographic variation in diapause of *Trichogramma dendrolimi*. Environmental Entomology, 46(6), 1302–1310. https://doi.org/10.1093/ee/nvx171

Zhang, F., Liu, M., & Li, Y. Y. (2018). Transcriptomic profiling of diapause in *Aphidius gifuensis*. Insect Science, 25(2), 234–246. https://doi.org/10.1111/1744-7917.12421

Zhang, F., Zang, L. S., & Desneux, N. (2022). Shelf-life technologies for parasitoids. Pest Management Science, 78(3), 1134–1145. https://doi.org/10.1002/ps.6809