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ADAPTIVE ENERGY ALLOCATION DURING INSECT DIAPAUSE: INSIGHTS AND IMPLICATIONS

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Diapause, a crucial behavioral adaptation in insects, entails metabolic challenges due to limited food resources, necessitating energy reserves buildup, particularly in the fat body and a reduction in body water content before entering diapause. Survival hinges on adequate energy reserves, prompting insects to curtail energetically costly functions like metamorphosis, long-distance flight, and reproduction. In diapause, insects dynamically manage energy utilization, possibly sensing metabolic reserves to determine diapause initiation and duration. Climate change impacts diapause, as rising temperatures escalate metabolic rates, tightening energy budgets. While the molecular mechanisms of nutrient regulation in diapause remain unclear, insulin signaling is pivotal. Photophase and scotophase durations influence diapause onset. Certain metabolites, such as TCA cycle intermediates, can deter diapause, hinting at potential pest management strategies. Further research into these mechanisms promises insights into insect survival strategies and improved pest control methodologies.

Diapause is a state of arrested development in insects, enforced by physiological mechanisms rather than concurrent unfavorable environmental conditions. It is characterized by low metabolic rates, oxygen consumption, body weight, water content, and vitamin deficiency. Coined by William Wheeler in 1893, the term "diapause" originates from the Greek "diapausis," meaning "pause". Historically, diapause's various phases have been studied since the early 20th century. Terms related to diapause include dormancy, quiescence, and diapause itself, the latter being a highly evolved form of dormancy to overcome cyclic and extreme environmental conditions. Thus, it is a vital survival strategy for insects, allowing them to withstand adverse environmental conditions and ensuring their species' continuation through generations.

Basic Classification of Diapause

- Diapause is classified based on seasonal variation and the influence of environmental factors. Aestivation occurs in response to higher temperatures (summer diapause), while hibernation occurs due to lower temperatures (winter diapause). For example, the spotted stem borer undergoes hibernation in North India and aestivation in South India.
- Based on environmental influence, diapause is classified into facultative and obligatory types. Facultative diapause occurs due to unfavorable environmental conditions and ends when conditions become favorable. Obligatory diapause is hereditary and species-specific, controlled by genes.
- Diapause also varies according to the life stage of the insect. Egg diapause is found in species like the mulberry silkworm, grasshoppers, and locusts, while larval diapause occurs in insects like the pink bollworm and maize stem borer. Pre-pupal diapause is observed in the Indian meal moth, pupal diapause in the cabbage butterfly and red hairy caterpillar, and adult diapause in species such as the white grub and mango nut weevil. Imaginal diapause is seen in mosquitoes.

Phases of Diapause

Insect diapause encompasses three phases, as outlined by Kostal *et al*. (2004):

1. **Prediapause:** Consisting of two sub-phases: a) **Induction Phase:** Genotype-specific ontogenetic stages trigger cues from the environment to switch from direct development to diapause. b) **Preparation Phase:** Occurs after induction, involving covert programming for diapause expression, including behavioral and physiological changes.
2. **Diapause Phase:** Further divided into three sub-phases: a) **Initiation Phase:** Direct development ceases, followed by metabolic suppression, while diapausing stages may continue feeding and preparing for adversity. b) **Maintenance Phase:** Endogenous arrest persists under favorable conditions, with specific stimuli helping to maintain diapause intensity. c) **Termination Phase:** Environmental changes trigger a decrease

in diapause intensity, synchronizing populations for overt or covert resumption of development.

3. **Post-diapause Phase:** Follows diapause termination, characterized by exogenously imposed inhibition of development and metabolism, allowing for reorganization before full activity resumes.

Endocrine System Involved in Insect Diapause

The insect endocrine system plays a crucial role in regulating diapause. Key hormones include juvenile hormone (JH), diapause hormone (DH), and prothoracicotropic hormone (PTTH). DH, primarily in *Bombyx mori*, induces diapause, while PTTH stimulates prothoracic glands to produce ecdysteroids for development. The corpora allata produces JH, critical for development. In *Riptortus pedestris*, pars lateralis neurons inhibit JH production, maintaining reproductive diapause. Absence of JH in adults leads to muscle degeneration and reproductive tissue atrophy, halting mating. JH presence in larvae prevents molting, and in *Diatraea gradiosella*, it facilitates fat body protein accumulation for diapause. DH regulates embryonic diapause in *Bombyx mori* by triggering glycogen conversion into sorbitol and glycerol, inhibiting embryo development. Glycerol and sorbitol revert to glycogen at diapause termination.

Consequences of Energy Shortfalls and Abundance

The energy reserves an insect can affect the decision to enter diapause, the decision to terminate diapause, and fitness during the postdiapause period. If insects that have not sequestered sufficient reserves to survive a lengthy diapause have four options: firstly they will die during diapause or post diapause development when all reserves have been depleted; secondly they have choice to avert diapause, an attempt to produce one more generation is a better option than dying; thirdly they terminate diapause prematurely when energy reserves become dangerously low; or lastly compensate for this deficiency by feeding during diapause.

Mechanisms Related to Diapause in Insect

In diapausing insects, energy sensing and insulin sensing mechanisms are crucial for assessing nutrient levels and regulating metabolic processes. Al-Anzi *et al.* (2009) found that fat bodies play a critical role in nutrient sensing and homeostasis. They identified specific neurons in Drosophila melanogaster that regulate feeding and nutrient balance. Baker and

Thummel (2007) studied the insulin-like peptide (ILP) pathway, which affects growth, reproduction, and metabolism. Disruption of insulin signaling in D. melanogaster inhibits reproduction and increases energy stores. The fork-head transcription factor (FOXO) is involved; in the presence of insulin, FOXO is suppressed, while its absence leads to fat accumulation.

Factors Affecting Insect Diapause

Environmental cues such as photoperiod, temperature, food availability and quality, host plant condition and parental rearing conditions collectively influence the induction or termination of diapause in insects. Photoperiod, the alternating light-dark phases in a day, is a primary cue, with changes triggering diapause onset or cessation. Temperature fluctuations, including thermoperiods, also impact diapause phases; for instance, chilling periods may signal the end of diapause in certain species like the woolly bear caterpillar. Food scarcity can induce diapause, as seen in the green lacewing and stem-boring moths. Additionally, host plant conditions can influence diapause induction. Parental rearing conditions, exemplified by the brown locust, may also play a role in diapause regulation, affecting the proportion of diapaused eggs laid. Overall, these factors, along with genetic predispositions, collectively control insect diapause.

Intensity of Diapause

Insect diapause exhibits significant variability in intensity, often measured by the duration of the diapause period. Typically lasting 9-10 months in temperate zones, diapause can extend for over a year in some cases, termed prolonged or extended diapause. Remarkable instances include the yucca moth with adults emerging after 19 years of diapause and wheat-blossom midges larvae overwintering for up to 12 years before adult emergence. Some sawflies show diapause stages lasting 3-4 years.

Use for Pest Control

Research indicates that diapause in insects involves a decrease in the release of certain intermediates from the fat body, leading to reduced activity in the tricarboxylic acid (TCA) cycle in the brain. Injecting diapause-programmed pupae with a mixture of four metabolites, including two TCA cycle intermediates, can prevent diapause and promote normal development. Glucose alone does not have this effect; the entire mixture is necessary. These findings suggest that metabolic intermediates play a crucial role in determining developmental outcomes. In simpler terms, disrupting the TCA cycle intermediates can abort diapause. Since diapause serves as a protective mechanism against environmental changes for many insect pests, interrupting it could lead to their demise, making it a potential method for pest control.

Conclusion

Insects predominantly store energy in the form of triacylglycerides, supplemented by glycogen reserves and hexameric storage proteins. Metabolic depression, induced by varying temperature conditions, is crucial for conserving these energy stores. The energy sensing mechanism plays a significant role in regulating the storage of diapause energy reserves. However, diapause negatively impacts key biological parameters including developmental duration, fecundity, progeny survivorship, egg viability, adult longevity, and reproductive behavior. Nonetheless, exclusion of diapause using specific metabolites presents a potential avenue for intervention and pest control strategies.

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