Insect Diapause

Our highly seasonal world restricts insect activity to brief portions of the year. This feature necessitates a sophisticated interpretation of seasonal changes and enactment of mechanisms for bringing development to a halt and then reinitiating it when the inimical season is past. The dormant state of diapause serves to bridge the unfavorable seasons, and its timing provides a powerful mechanism for synchronizing insect development. This book explores how seasonal signals are monitored and used by insects to enact specific molecular pathways that generate the diapause phenotype. The broad perspective offered here scales from the ecological to the molecular and thus provides a comprehensive view of this exciting and vibrant research field, offering insights on topics ranging from pest management, evolution, speciation, climate change, and disease transmission, to human health, as well as analogies with other forms of invertebrate dormancy and mammalian hibernation.

David L. Denlinger is one of the world’s leading researchers on insect diapause. He is a Distinguished University Professor and Professor Emeritus of Entomology at The Ohio State University, USA. He is a member of the National Academy of Sciences, a Fellow of the Entomological Society of America, and an Honorary Fellow of the Royal Entomological Society. Professor Denlinger’s current laboratory research focuses primarily on molecular mechanisms involved in insect overwintering. His interests range from the use of clock genes to perceive environmental signals through the endocrine and molecular events that result in the expression of the diapause phenotype. He has received numerous awards for his research, including the Gregor Mendel Medal from the Czech Academy of Sciences (2006), the Antarctic Service Medal (2006), and the International Centre of Insect Physiology and Ecology (ICIPE) Achievement Award (2020).

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To every thing there is a season

Ecclesiastes 3:1

The surge of new plant growth in the spring is followed quickly by a flush of insects that exploit those plants for food. And then, just as quickly, as summer wanes and winter approaches, plants die back and insects disappear until the cycle repeats the following year. Ours is a highly seasonal world. The tilt of the Earth as it circles the Sun dictates the intensity of heat impinging on the Earth's surface, thus driving the striking seasonal rhythms of life. Temperature contrasts between winter and summer are dramatic, and even in the tropics, where temperatures remain more constant, wet and dry seasons pose a conspicuous seasonal pattern. The impact this has on all life forms is consequential, but the challenge is especially pronounced for insects and other arthropods that, as ectotherms, can perform only within a narrow seasonal window. Escaping in time thus becomes an essential and crucial feature of the insect life cycle, allowing insects to survive seasons that are too cold, too dry, or lacking essential food resources required for development and reproduction.

Diapause, a dormant stage akin to mammalian hibernation, thus emerges as a key feature that may encompass the major portion of an insect's life. Development is shut down or dramatically retarded, allowing the insect to bridge inimical seasons. The ability of insects to avoid such unfavorable seasons by entering diapause has made it possible for this group of animals to not only invade all seven continents but also become the dominant life form in most of Earth's terrestrial habitats. Insects, of course, are not alone in their ability to respond to seasonal changes in the environment, but the diversity of insects, our ability to experimentally manipulate their environment, and our growing understanding of insect molecular processes have made insects a particularly rich taxon for probing seasonal responses. How an insect knows when bad times are coming, why and how it responds to evoke the diapause response, and the consequences of diapause for post-diapause development is the story I hope to relay.

Several wonderful reviews greatly influenced my understanding of diapause down through the years. My first encounters as a student with the diapause literature were delightful treatises by A.D. Lees (1955) entitled *The Physiology of Diapause in Arthropods* and by A.S. Danilevskii (1965 translation from Russian) entitled

Photoperiodism and Seasonal Development of Insects. This was followed by books that I eagerly devoured by S.D. Beck (*Insect Photoperiodism*, 1968); D.S. Saunders (*Insect Clocks*, 1976 [2002]); M.J. Tauber, C.A. Tauber, and S. Masaki (*Seasonal Adaptations of Insects*, 1986); and H.V. Danks (*Insect Dormancy: An Ecological Perspective*, 1987). The quality of these remarkable books makes it a bit daunting to consider adding my own perspective, but do so, I will! These previous books on insect diapause contain great background information on diapause as well as lists of diapausing insects that I will not repeat here, but instead, I hope to highlight major features of diapause with special emphasis on recent developments in the field.

In spite of the diversity of insects, quite a few common themes unite diapause responses observed across a range of species. I offer some hints on the diversity of responses, but I err on the side of giving more depth to some of the best-studied models at the expense of portraying all the variants. I place special emphasis on flies and moths, a bias that comes from my life experiences with these two prominent groups.

I am enormously grateful to my mentors who introduced me to diapause and encouraged me along the way. My graduate advisors, Gottfried Fraenkel and Judith Willis, introduced me to flesh fly diapause and the broader realm of diapause physiology; my postdoctoral advisor Jan de Wilde shared his diapause expertise and dared to send this Pennsylvania Dutchman to Kenya as a Dutch representative to explore diapause in the tropics; and Carroll M. Williams provided an engaging laboratory, replete with a rich history of diapause experimentation, when I returned to North America. I am also enormously grateful to all the students, postdocs, and visiting scholars who have been through my laboratory at Ohio State and contributed so much to my own understanding of diapause. While I often got the credit, it was their hard work that allowed us to deepen our understanding of diapause mechanisms. And, more broadly, the entire diapause community has attracted a great cadre of people with whom I have enjoyed interacting. Thanks for all you have taught me. I hope I have captured your insights correctly.

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