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RESEARCH ARTICLE

Transcriptomic and proteomic analysis of *Locusta migratoria* eggs at different embryonic stages: Comparison for diapause and non-diapause regimes



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Abstract

Temperate-zone insects typically survive winter by entering diapause. Although many aspects of insect diapause have been studied, the underlying molecular mechanism of insect diapause is not well understood. Here we report the results of the transcriptional and translational differences of migratory locust eggs at different embryonic states using diapause (low temperature) and non-diapause (high temperature) regimes. Compared with non-diapause eggs at 100 degree-days (N2) treatment, 29671 transcripts and 296 proteins were differentially expressed at the diapause maintenance stage (D2). While compared with 150 degree-days (N3) treatment, 45922 transcripts and 404 proteins were differentially expressed in the post-diapause stage (D3). Among them, 51 and 102 transcripts had concurrent transcription and translation profiles in D2 vs. N2 and D3 vs. N3 treatments, respectively. Analysis of Gene Ontology categorized these genes and proteins into three categories: biological processes, cellular components, and molecular functions. Biological pathway analysis indicated that three pathways: (1) insect hormone biosynthesis (KEGG: Map 00981), (2) the insulin signaling pathway (KEGG: Map 04910), and (3) the peroxisome proliferator-activated receptor (PPAR) signaling pathway (KEGG: Map 03320) play an important role in locust diapause regulation. Most of these transcripts and proteins were up-regulated in the diapause treatments, and were highly linked to juvenile hormone biosynthesis, insulin and PPAR signaling pathways, suggesting these three pathways may be involved in diapause and development regulation. This study demonstrates the applicability of high-throughput omics tools to identify biochemical pathways linked to diapause in locust egg development. In addition, it reveals that cellular metabolism in diapause eggs is more inactive than in non-diapause eggs, and most of the down-regulated enzymes and pathways are related to reduce energy loss.

Keywords: *Locusta migratoria*, diapause, transcriptome, proteome, molecular mechanism

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1. Introduction

To survive harsh winter conditions, many temperate-zone terrestrial invertebrates enter diapause, a protective physiological state in which activity, growth, development, and metabolic rates are dramatically lowered, and cryoprotectant

compounds produced (Denlinger 2002; Liu *et al.* 2014). Diapause is an evolved and adaptive form of phenotypic plasticity, during which a set of alternative genetic programs are run. Diapause can be obligatory (i.e., it is a mandatory, genetically fixed component of ontogeny, and mostly unresponsive to environmental stimuli) or facultative (i.e., its occurrence and nature are influenced by current and/or previous environmental conditions), depending on species and population (Uvarov 1966, 1977; Chen 2007; Whitman and Ananthakrishnan 2009). Diapause is vitally important for temperate-zone insects because it determines their overwintering survival and distribution. In other words, poor synchrony between the timing and nature of diapause and local winter conditions can devastate a population. Understanding diapause is essential for predicting future phenology, invasion, and population densities of insect pests, and is a critical component of insect pests management.

Although many aspects of diapause are well-known, the molecular mechanisms of diapause maintenance and post-diapause stages have been elucidated, which has been aided in large part by the “omics” revolution (Colinet *et al.* 2012; Stuckas *et al.* 2014). Indeed, understanding the molecular mechanism of diapause (gene regulation, signaling pathways, biochemical cascades, hormonal regulation, etc.) is the last remaining component for fully understanding this complex and important developmental process (Whitman and Ananthakrishnan 2009). In this paper, we report the results of a large-scale analysis of transcriptional and translational differences between diapause and non-diapause eggs of the migratory locust, *Locusta migratoria* L., an important pest of crops in China (Chen 2007; Stuckas *et al.* 2014). Voltinism in this sub-species varies geographically. In South China, warm temperatures and long growing seasons allow 3–4 generations per year; however, in North China, short and cool seasons allow for far fewer generations (1 or 2) per year (Tanaka 1994; Tanaka and Zhu 2008). In the field, locusts bury the egg pods 1–3 cm below the ground. During warm summer weather, the eggs hatch in approximately 16 days; however, when eggs are laid during cooler temperatures in late fall, they enter diapause and do not hatch until spring. Hence, the eggs of this sub-species exhibit facultative diapause, whereby the decision to enter or not enter diapause is determined, in part, by a combination of maternal temperature and incubation temperature (Hakomori and Tanaka 1992; Tanaka 1992). Before diapause stage, the embryo develops continuously at a relatively high temperature but enters diapause at a lower temperature (Tanaka 1992). In *L. migratoria*, diapause occurs during the anatrepsis stage of embryonic development. Both diapause and non-diapause embryos develop up to the point of anatrepsis, but non-dia-

pause eggs continue their rapid development to maturity and hatching, whereas diapause eggs halt development, and remain static at the anatrepsis stage for 3 months. Diapause in *L. migratoria* complex, and additional factors influence diapause and duration of the egg stage, including maternal effect, photoperiod, incubation temperature, soil moisture, quiescence, and gene (Tanaka 1994). Interestingly, different populations of *L. migratoria* have evolved different diapause responses (Guo *et al.* 1991), but the molecular biology of different diapause stages has yet to be investigated (Kislinger *et al.* 2006; Carolan *et al.* 2011).

In this study, we performed a comparative analysis of transcriptomes (RNA-seq) and proteomes (iTRAQ) of diapause and non-diapause eggs, and evaluated the difference between our conclusions in this study at the diapause maintenance and post-diapause stages with our prior research involving locust pre-diapause stage (Tu *et al.* 2015). Our goal is to understand the complex genetic and molecular events which underlie diapause in order to better combat this devastating agricultural pest.

2. Materials and methods

2.1. Insect materials

Eggs were collected from the field at Tianjin, China (38°49'N, 117°18'E) in November 2007, and brought to the Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing.

2.2. Insect growth conditions

To obtain diapause and non-diapause eggs, we raised oriental migratory locusts in growth cabinets (PRX-350B-30; Beijing Kelin Hengda Technology Development Co., Ltd., China) under low and high temperature regimes. The daily temperature in field, from 16 July to 6 November 2012, was recorded and used as a reference (reference value) to artificially mimic the natural daily temperature cycles for the high temperature regime (reference value+1), and the low temperature regime (reference value-1) in temperature controlled growth cabinets. The photoperiod regime used in the experiment was 12 h L and 12 h D, and the relative humidity (RH) was kept at ~60% for eggs and ~80% for nymphs and adults. We recorded temperature data 24 h per day for each growth cabinet using a HOBO Pro V2 logger (Onset Computer Corporation, USA). The results showed that the degree-days (DD) of the high temperature regime was 840 heat units and the DD of the low temperature regime was determined to be 678 heat units (Tu *et al.* 2015).

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