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Prepupal diapause and instar IV developmental rates of the spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae)

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ABSTRACT

The spruce beetle, *Dendroctonus rufipennis* (Kirby), is an important mortality agent of native spruces throughout North America. The life-cycle duration of this species varies from 1 to 3 years depending temperature. The univoltine cycle (one generation per year) is thought to maximize outbreak risk and accelerate host mortality in established outbreaks. Prepupal diapause is associated with the semivoltine cycle (one generation per 2 years) and we investigated thermal conditions that result in diapause induction. Preliminary experiments used respirometry in an attempt to distinguish the diapause state of experimental insects but the technique was apparently confounded by low respiration before and during pupation, regardless of diapause status. Therefore, diapause induction was deduced using developmental delays. The observed developmental response was not a "switch", with developmental delay either present or absent, but instead varied continuously. We found that temperatures <15 °C from instar III through mid-instar IV were associated with developmental delays beyond that expected from cool temperatures. Moreover, the duration of exposure to cool temperatures was important in determining the degree of developmental delay. Small, if any, delays were observed if the cumulative exposure to <15 °C was <20 d whereas >40 d cumulative exposure was associated with distinct developmental suppression. Intermediate exposure to cool temperatures resulted in minor developmental delays. We used our results to parameterize a maximum likelihood estimation model of temperature-dependent instar IV developmental rates, including the effect of diapause. This model can be included as part of a spruce beetle phenology model for predicting population dynamics.

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1. Introduction

Insect life-cycles are shaped by the seasonality of their environment. In response to seasonally predictable, yet unfavorable environmental conditions, many insect species have evolved a diapause syndrome wherein physiological, behavioral, and/or morphological adaptations enable survival during adverse conditions and facilitate ecologically appropriate timing of life-cycle events (Tauber et al., 1986). To survive adverse conditions, insects must predict, rather than monitor, seasonal changes using signals that are reliable, frequent, and recognizable (Danks, 1987). Photoperiod, or the length of day, is invariant from year to year and is often used by insects as a cue to adjust life-cycle events in advance of adverse conditions (Danilevsky, 1965). Other signals, including temperature, moisture, and food are used by some species either alone or in conjunction with day length to keep track of seasonal time, especially in environments where day length changes are not detectable (Danks, 2007). There are some insect species where diapause induction is a response to daily temperature cycles (i.e., thermoperiods) in constant darkness (Beck, 1980). Because diapause can alter life-cycle timing and duration, knowledge of the conditions that induce or avert diapause is imperative in models developed for predicting population-level dynamics of economically and ecologically important insects.

The spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae, Scolytinae), is an important mortality agent of spruces, *Picea* spp. (Pinaceae), throughout its hosts' ranges in North America. Wide-spread and severe outbreaks have occurred in the recent past in Alaska (Holsten et al., 1999), Utah (Dymerski et al., 2001), and the Yukon Territory (Parks Canada, 2009). The spruce beetle has a highly variable life-cycle, with durations of 1–3 years although the semivoltine cycle is most common (Knight, 1961). Summer temperature has repeatedly been shown to be strongly correlated with spruce beetle life-cycle duration (Massey and Wygant, 1954; Dyer, 1969; Werner and Holsten, 1985; Hansen

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et al., 2001a). Outbreak potential is heightened when univoltine broods are produced (Reynolds and Holsten, 1994; Hansen and Bentz, 2003; Berg et al., 2006).

Spruce beetles emerge from host trees in late spring to infest new host trees, mate, and oviposit eggs in the phloem layer beneath the bark where larval development through four instars occurs throughout the summer. Relatively warm summer temperatures increase the probability that development will progress to the pupal and adult stages prior to winter, resulting in the univoltine life-cycle. If sufficient development does not occur prior to the beginning of reduced temperatures in the fall, spruce beetles enter a prepupal diapause for the winter, resulting in the semivoltine cycle. This diapause was first demonstrated by Dyer (1970). Larvae reared in relatively cool thermoperiod regimes experienced developmental delay during instar IV compared to insects reared at a constant 21.1 °C; the degree of delay was considerably longer than was expected from, simply, the lower temperatures. Dyer and Hall (1977) found additional evidence for diapause and proposed that temperatures below 15.1 °C during instar III will induce diapause during instar IV. Hansen et al. (2001b) found little evidence of diapause induction during instar III, but did find two lines of diapause evidence in a series of constant-temperature rearing experiments. First, the temperature-dependent developmental rate of instar IV was not well represented by a continuous function, as with other lifestages, having a notable disconnect between rates above and below 15 °C. Second, there was a dramatic difference in instar IV developmental times at 15 °C depending on whether larvae were reared at constant 15 °C from the egg stage or pre-conditioned at 21 °C into instar III. Namely, two of 15 larvae reared at 15 °C beginning as eggs developed similarly as the 21 °C pre-conditioned group (pupating within 29 days) whereas the other 13 failed to pupate after as long as 142 days when the experiment was ended. From their results, Hansen et al. (2001b) hypothesized that diapause is induced later in the life-cycle than instar III, possibly during the late instar IV or early prepupal phase.

Both univoltine and semivoltine spruce beetle have been found developing in the same host tree (Hansen et al., 2001a), indicating phenotypic plasticity for the trait and suggesting that microhabitat temperature plays a large role in diapause induction. Because the spruce beetle spends all but a few days of its life-cycle beneath the bark of a host tree, photoperiod may not be a major controller of diapause in this insect, although photoperiod has never been explicitly tested independent of temperature cues. Temperature cues, however, have been shown to induce diapause independent of photoperiod (Dyer, 1970; Dyer and Hall, 1977; Hansen et al., 2001b).

Our objective was to describe and model the lifestage-dependent conditions associated with prepupal diapause induction in spruce beetle. This information can ultimately be used in a lifestage-specific spruce beetle phenology model allowing for detailed predictions of population response to thermal conditions. Specifically, we investigated: (1) whether prepupal diapause induction is influenced by photoperiod; (2) the effect of instar IV maturity on diapause induction; (3) thermocycle (i.e., temperature-only aspect of a thermoperiod, with thermophase and cryophase durations held constant) conditions associated with diapause induction focusing on cryophase temperatures; and (4) diapause expression as a function of interactions among temperature, lifestage during low temperature exposure, and duration of low temperature exposure. We conducted five experiments, the first three to determine basic parameters associated with diapause induction and, based on the results thereof, two additional experiments to investigate interactions of temperature, larval maturity, and duration of exposure to low temperatures. We also developed a model for estimating instar IV temperature-dependent developmental rates as a function of diapause inducing conditions during instars III and IV.

2. Materials and methods

2.1. Phloem sandwiches

For all experiments, larvae were reared in 15 × 15 cm phloem sandwiches which enable visual inspection of lifestage change on a daily basis (Bentz et al., 1991; Hansen et al., 2001b). Parent spruce beetles came from an infested Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.), cut from the Fishlake National Forest, Utah (38° 37.424′ N; 111° 59.188′ W), 27 September 2006. Infested bolts were stored at 0 °C until use. An uninfested Engelmann spruce was cut from the Cache National Forest, Utah (41° 37.243′ N; 111° 26.002′ W), 17 October 2006. As needed, infested bolts were placed in rearing cans at room temperature, emerged adults collected, and female–male adult pairs were manually inserted into bolts from the uninfested spruce. After 7–10 days, eggs were collected from the distal portion of each gallery in an effort to obtain relatively fresh eggs of similar age. Twelve eggs were inserted into separate niches of each phloem sandwich. Sandwiches were held in constant humidity desiccators which were kept in environmental chambers (Percival Scientific, Inc., Perry, Iowa; Gray et al., 1998). Environmental chambers were calibrated to within 0.1 °C of the target temperature as monitored by an independent datalogger (Campbell Scientific, Inc., Logan, Utah). Larval instar was distinguished based on head-capsule width (Hall and Dyer, 1974) and the transition between instars was marked by cast head-capsules following molting. Some larvae were occasionally not visible as they submerged into the phloem, and observations were omitted if the specific date of molting or pupation could not be determined.

2.2. Evaluation of the diapause state

Reduced respiration is often used as an indication of the diapause state (Danks, 1987; Tauber et al., 1986). To evaluate the use of respiration for detecting prepupal diapause in the spruce beetle, we conducted two preliminary laboratory experiments. In the first experiment, larvae were reared in a thermocycle regime that simulated phloem temperatures recorded at a field site where the semivoltine life-cycle was observed (Hansen et al., 2001a), i.e., conditions associated with prepupal diapause. Instar IV larvae and prepupae were periodically sampled from thermocycle-treated bolts and allowed to equilibrate for 1 h at 20 °C before conducting constant volume respirometry (PTC-1 temperature cabinet and PELT-3 controller, Sable Systems International, Las Vegas, Nevada). Larvae and prepupae were placed individually into glass respirometry chambers attached to a CO_2 analyzer (Sable CA-1B, Sable Systems International, Las Vegas, Nevada). Respiration, expressed as CO_2 output, was measured at 20 °C after an additional 60 min. Data acquisition and constant volume calculations were made, respectively, with DATACAN and CONVOL software (Sable Systems International, Las Vegas, Nevada). Prepupae were weighed (±0.001 mg; Cahn C-33, Thermo Orion, Beverly, MA) to calculate fresh weight standardized expression of respiration, $\mathrm{ml\,CO_2\,g^{-1}\,h^{-1}}$. Results showed markedly reduced respiration as the prepupal stage was attained during September and respiration remained low through June; a U-shaped pattern over time consistent with other diapausing insects (Danks, 1987). We did not, however, compare rates to a reference treatment without other evidence of diapause, i.e., one wherein developmental delays were not observed.

A second experiment was conducted using larvae reared at either constant 12 or 18 °C. Respiration rates of prepupae were measured as described above. We found no significant respirometry

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