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Research Paper

Host utilization, reproductive biology, and development of the larval parasitoid *Tetrastichus planipennisi* as influenced by temperature: Implications for biological control of the emerald ash borer in North America

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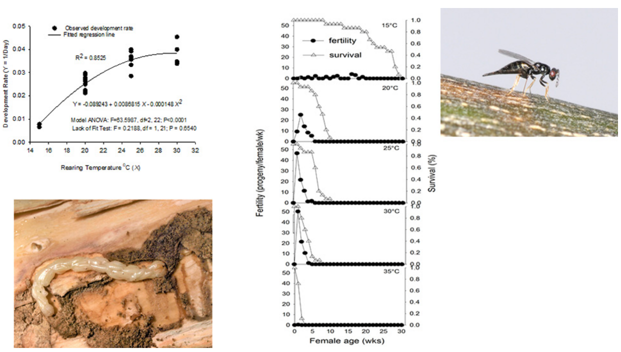
GRAPHICAL ABSTRACT



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ABSTRACT

The success of classical biological control programs depends in part on understanding climate effects on introduced agents. *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae), a larval endoparasitoid of emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is being introduced to EAB-invaded regions of the United States (USA) and Canada for biological control. To optimize regional release strategies and increase efficiency of the EAB-biocontrol program, we determined the effects of five constant temperatures from 15 °C to 35 °C on *T. planipennisi* parasitism rate, development, adult longevity, and fecundity in EAB. Results showed a decrease in parasitoid development time from 139.8 days at 15 °C to 26.3 days at 30 °C, while no parasitoid eggs hatched at 35 °C. Parasitism rates, provisioned with an excess of host larvae throughout their life, increased from 1.4% at 15 °C to 28% at 30 °C then declined to 0.5% at 35 °C. Adult parasitoid longevity declined from 24 weeks at 15 °C to < 2 weeks at 35 °C. Fertility table analyses revealed *T. planipennisi* net reproductive rate was highest at 25 °C, and intrinsic and finite rates of increase were highest at 30 °C, suggesting 25–30 °C as optimal rearing temperatures for this parasitoid. Combining these results with temperature data from climate zones of 3–7 in the USA, we predicted *T. planipennisi* can complete more than one generation in all locations in these climatic zones, with more generations in warmer climates. Moreover, our findings also suggest that despite the availability of suitable EAB larval stages for parasitism, releases of *T. planipennisi* in early spring or late fall in

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cold climate zones may be suboptimal due to low temperatures, as may mid-summer releases in hot climate zones due to high temperatures.

1. Introduction

Classical biological control is an ecologically-based tool that can be used for the long-term management of invasive pests. The success of classical biological control programs hinges on the establishment of specialized natural enemies introduced from the native range of the invasive pest. To increase the probability that these natural enemies establish after introduction to new regions, it is important to have an in-depth understanding of how climatic factors influence the development and reproductive biology of the agents (Hoelmer and Kirk, 2005). Parasitic wasps, or parasitoids, are often used as biocontrol agents of invasive insect pests. Because parasitoids like other insects are poikilothermic, ambient temperatures directly affect their developmental rates, reproduction, mortality, body size, and/or behavior (e.g. Howe, 1967; Atkinson, 1994; Wang et al., 1999; Golizadeh et al., 2009; Mawela et al., 2013; Rodrigues et al., 2013; Yu et al., 2013). Knowledge of temperatures that favor the development and rapid population growth of insect natural enemies is important not only for optimizing biocontrol agent release strategies (Pilkington and Hoddle, 2006), but also improving the efficiency of natural enemy mass-rearing programs (e.g., Qiu et al., 2012; Favero et al., 2015). Moreover, the likelihood of natural enemy establishment in the newly introduced region may reasonably be predicted if it is known how temperature affects key parameters of its development, reproduction, biology, and population growth (Pilkington et al., 2014).

Tetrastichus planipennisi Yang (Hymenoptera: Eulophidae) is a specialized larval endoparasitoid of the emerald ash borer (EAB), *Agrilus planipennis* Fairmare (Coleoptera: Buprestidae), and plays an important role in regulating the pest population in its native range of northeast Asia (Liu et al., 2003, 2007; Wang et al., 2015). In 2007, five years after EAB was first detected in the United States (USA), this parasitoid, along with the egg parasitoid *Oobius agrili* Zhang & Yang and the larval ectoparasitoid *Spathius agrili* Yang, were first introduced from northeast China to the USA as EAB biocontrol agents (Federal Register, 2007). The initial releases of these three EAB parasitoid species (*T. planipennisi*, *O. agrili, S. agrili*) were made in Michigan, the epicenter of EAB invasion, and only a few hundred of each species were released due to limitations in insect rearing. After USDA initiated the EAB Biocontrol Program and a mass-rearing facility became operational in 2010, larger numbers of parasitoids became available for release at more sites (Bauer et al., 2014, 2015). To date, 27 of 33 United States and two of the three Canadian provinces with known EAB infestations have released one or more of the EAB biocontrol agents (Duan et al., 2018). Although these three biocontrol agents were recovered one year following their releases at some early Michigan study sites, only *T. planipennisi* and *O. agrili* are consistently recovered and expanding their range in EAB populations (Bauer et al., 2015; Duan et al., 2018).

While the role of the egg parasitoid *O. agrili* in suppressing EAB population growth remains to be determined, *T. planipennisi* appears to play a significant role in suppressing EAB population growth in young ash trees and saplings in long-term study sites in Michigan (Abell et al., 2014; Duan et al., 2013a, 2015, 2017). However, parasitism rates by *T. planipennisi* varied among different geographic regions in the USA. For example, the average parasitism rates of EAB larvae by *T. planipennisi* (sampled in the fall and early spring) was approximately 11% in Maryland (Jennings et al., 2016), 10.5% in Kentucky (Davidson & Rieske, 2016), and approximately 30% in Michigan (Duan et al., 2013a, 2015, 2017). In northeast China, where *T. planipennisi* was originally collected, the parasitism rate of EAB larvae sampled in late summer and fall averaged ~40% (Liu et al., 2007). It is not known if key climatic factors such as temperature may contribute to geographic, seasonal, and year-to-year variations in parasitism rates of EAB larvae by *T. planipennisi*.

A previous study determined some critical life-history parameters relating to immature larval development and adult reproduction of *T. planipennisi* at constant 25 °C (Duan et al., 2011). More recently, a laboratory flight-mill study showed that ambient temperatures strongly affected the flight distance and speed, and post-flight mortality of adult *T. planipennisi* (Fahrner et al., 2015). To date, however, no studies have reported on temperature ranges that optimize parasitism rates, development, reproduction, and population growth of *T. planipennisi*.

In the present study, we determined the effects of different temperature ranges (15 °C–35 °C), which might occur during the growing season (May to September) in the USA, on *T. planipennisi*'s host parasitism rates, development and survivorship of its immature stages, as well as adult longevity and fecundity. Based on these laboratory results and location-specific climatic data, we then estimated the potential for *T. planipennisi* population growth in representative areas from climate zones 3 to 7 in the USA (USDOE, 2013), where EAB has invaded or has the potential to invade, and biocontrol has been or could be implemented (MapBiocontrol, 2017; USDA APHIS, 2018). This information may improve the efficiency of mass-rearing and field release strategies for this important EAB biocontrol agent.

2. Materials and methods

2.1. Parasitoids

Tetrastichus planipennisi used in this study were F23 - F25 progeny of a laboratory colony that originated from parasitized EAB larvae collected in 2008 in Fengcheng, Liaoning province, China (Wang et al., 2015). This colony was maintained on EAB larvae infesting tropical ash [*Fraxinus uhdei* (Wenzig) Lingels] stems at the USDA ARS Beneficial Insect Introduction Research Unit, Newark, DE. Before being used in various experiments, newly emerging (< 3 d old) adult parasitoids were housed in ventilated acrylic cylinders (20 cm height × 12 cm diameter) using a 3:1 female:male (F:M) sex ratio and maintained in environmental chambers (AR-66L2, Percival Scientific, Perry, IA) at 25 ± 1.5 °C, 65 ± 10% RH, and 16:8 h (L:D) photoperiod. From field collections and laboratory rearing, 2.5:1 F:M is the typical sex ratio for *T. planipennisi*, and each male mates with multiple females (Yang et al., 2006; Duan et al., 2011; Duan and Oppel, 2012). A water source was provided inside each acrylic cylinder via a 37-ml clear plastic vial (US Plastics, Lima, OH) fitted with a 10-cm braided cotton dental wick (Richmond Dental, Charlotte, NC), and clover honey was streaked on the ventilation screens of rearing containers as a food source.

2.2. Host larvae

Host EAB larvae used in this study were 3rd–4th instars reared in tropical ash stems (14 cm length × 1–3 cm diameter) (Duan et al., 2013b). Briefly, EAB eggs laid on unbleached coffee filter paper (HOMELIFE, Eden Prairie, MN) were placed onto ash stems in single or pair groups against the surface of the wood and held on with strips of Parafilm® (Bemis Co., Inc., Neenah, WI). After infestation with EAB eggs, the ash stems were placed in water-soaked floral foam bricks (OASIS®, Smithers-Oasis Co., Kent, OH) inside plastic containers ($58.4 \times 41.3 \times 31.4\ cm^3$, Sterilite Corp., Townsend, MA) and incubated in an environmental chamber at 27 ± 1.5 °C, 65 ± 10% RH, and 16:8h (L:D) photoperiod for 4.5–5 weeks to produce the suitable