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Temperature-dependent response of diapause termination in emerald ash borer (Coleoptera: Buprestidae): implications for its geographic distribution

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The emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), native to Northeast Asia, is the most destructive invasive pest of ash (*Fraxinus* spp.) in North America. In this study, we exposed mature fourth-instar diapausing EAB larvae (J-shaped or J-larvae) to nine temperatures ranging from 1.7 to 23.9 °C for 90 days, and then evaluated their diapause termination by measuring both the probability and timing of post-chill development to adults under warm rearing conditions (27 ± 0.5 °C, 16:8 h L: D). We also determined the effect of chill temperature on the mortality of diapausing J-larvae. Results showed that J-larvae successfully completed diapause after exposure to temperatures between 7.2 and 15.6 °C for 90 days and chill treatment significantly affected the duration required for post diapause development to adult emergence, with the mean number of days required for adult emergence increasing as chill temperature increased. In addition, the mortality rate for the EAB larvae that died at the J-larval stage before completing diapause development to adults was lower (0% to 7.1%) for temperatures between 1.7 and 12.8 °C than that (16% to 32.6%) for temperatures between 15.6 and 23.9 °C. These results refine our understanding of the thermal limits for EAB diapause termination and provide insight into how climatic conditions may influence EAB phenology and distribution across its geographic range.

Keywords: invasive species, overwintering, diapause, Buprestidae, *Agrilus planipennis*

Introduction

Emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is the most serious invasive forest insect pest that has invaded North America. Since its discovery near Detroit, MI, in 2002, EAB has spread to 38 U.S. states and 5 Canadian provinces in eastern North America and will likely continue to spread throughout the range of ash in North America (Canadian Food Inspection Agency 2026, Emerald Ash Borer Info 2026). The beetle has also spread rapidly in European landscapes. For instance, after the beetle was detected in Moscow in 2005 (Izhevskii and Mozolevskaya 2010), it has since spread northwest to St. Petersburg and southwest into Ukraine as far as Kiev (Drogvalenko et al. 2019, Musolin et al. 2021, EPPO 2023). The ongoing dispersal and establishment of this Asiatic beetle across both North America and Europe suggest that EAB can survive a broad range of climate conditions, including extreme winter cold events (Crosthwaite et al. 2011, Duell et al. 2022, Chandler et al. 2026). Although susceptibility varies amongst North American ash species to EAB attacks, EAB reproduction has been recorded in all ash species it has encountered to date, leaving multiple ash species at risk of functional extirpation.

EAB adults lay eggs in bark cracks or crevices of ash trees after they are sexually mature and have mated. Larvae hatch from eggs and tunnel into the cambial region where they feed through 4 instars (Chamorro et al. 2015). Upon reaching maturity, larvae construct pupal cells in the outer sapwood or in the outer bark if thick enough. They then fold into a characteristic J-shaped form within the pupal cell. This transformation to the J-larval stage typically occurs between late summer and late fall, at which point, EAB larvae are considered to have entered an obligatory diapause (Duan et al. 2021, Dang et al. 2025). Larvae that do not reach maturity (or J-larval stage) during their first season of development will overwinter in the cambial region and continue development the following spring and summer (Chamorro et al. 2015).

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For insects adapted to temperate climates, obligatory diapause can serve multiple physiological and phenological functions (von Schmalensee et al. 2024). The primary function is often to allow insects to survive unfavorable conditions, especially cold temperatures. However, because both univoltine and semivoltine EAB life cycles can occur and immature EAB larvae can successfully overwinter in the cambial region, the primary function of obligatory diapause in EAB appears to be the synchronization of adult development (Duan et al. 2021). This is necessary so that adult emergence of both univoltine and semivoltine individuals occurs when ash foliage is available during the spring and summer for adult maturation feeding and lifetime maintenance, but early enough in the season to allow EAB eggs to hatch and larvae to enter the cambial tissue of trees where they can survive winter conditions.

Before metamorphosis to the adult stage can begin, EAB J-larvae must experience a period of chill period to terminate obligatory diapause. Duan et al. (2021) determined that a minimum of 2 months at 12.8 °C was required for diapause completion with an optimal duration of 3 to 4 months. However, J-larvae held at 1.7 °C failed to terminate diapause. This suggests that diapause termination occurs only within a specific range of suitable temperatures that includes, but is not limited to, 12.8 °C.

The current latitudinal distribution of EAB in North American spans a wide range of climates (Emerald Ash Borer Info 2026). Although the reported distribution of EAB in Asia is somewhat broad, the population introduced into the U.S. originated in Northeast China (Bray et al. 2011). Moreover, recent surveys for viable populations across the southern extremes of EAB's reported distribution in Asia have been unsuccessful (Duan and Petrice, personal observation), suggesting that its southern distribution in its native range may be more restricted than what has been previously reported. Temperature requirements for completing (or terminating) diapause likely contribute to these distributional limits. In addition, winter temperature effects on diapause development may influence voltinism, adult emergence timing, and survival (eg, Duan et al. 2021; Chandler et al. 2026). Understanding how chill temperatures affect EAB diapause termination is therefore necessary for understanding its geographic distribution limit and phenology across different latitudes and climates and has important implications for its management. For example, the ability to predict emerald ash borer adult emergence is critical for timing both insecticide treatments and releases of the egg parasitoid *Oobius agrili*, an EAB classical biological control agent from Northeast Asia approved for release in North America. Accurate prediction of EAB adult emerge is also important for predicting subsequent seasonal larval development for synchronizing the releases of the introduced EAB larval parasitoids, *Spathius galinae* and *Tetrastichus planipennisi*, with susceptible EAB larval stages.

Here, we exposed EAB J-larvae reared in ash bolts to a series of chill temperature treatments for 90-days to induce diapause termination. After which, J-larvae were exposed to warm (normal) rearing conditions to allow for post-diapause development and adult emergence. Using data on adult emergence and surviving J-larvae at the end of study, we modeled the temperature-dependent response for EAB diapause termination (ie, probability of adult emergence) and determined the suitable and optimal range of temperature treatments for their diapause termination. In addition, we also determined the time of post-diapause development to adults under warm rearing conditions as well as mortality rates associated with each temperature treatment.

Materials and Methods

Rearing Mature (J-Shaped) EAB Larvae

All EAB larvae used for this study were mature J-shaped fourth instars (J-larvae) reared in bolts of tropical ash (*Fraxinus uhdei* (Wenzig) Lingelsh) or green ash (*Fraxinus pennsylvanica* Marshall) according to procedures described in Duan et al. (2021). We used freshy cut bolts from these 2 different ash species to rear EAB larvae to its mature stage (J-larvae) solely for logistical reasons. Both species have been used to rear EAB in our laboratory for more than a decade, and we have never observed any significant differences in diapause termination or J-larval mortality among larvae reared on bolts from these two species (Duan et al. 2013).

Adult EAB beetles (F_0) used for egg (F_1) production originated from infested green (*F. pennsylvanica*) or white (*Fraxinus americana* L.) trees harvested in Maryland. EAB-infested green or white ash trees were felled and cut to half-meter-long logs in the fall of 2021 or 2022 and stored in a climatically controlled walk-in cooler (Polar King International, Fort Wayne, IN) at ~7.2 °C (45°F) for 3 to 9 months prior to use for adult (F_0) production. For adult beetle production, field-harvested and cold-stored ash logs were placed into emergence cages made of cardboard Sonotube (1.2 m long by 50 cm in diameter), and then incubated at 26 to 27 °C with a long day photoperiod of 16:8 (L: D) hours in an environmentally controlled room. Newly emerged adult beetles were transferred to rearing containers (clear 3.5-liter clear plastic Jars with screen-ventilated lids) and reared for oviposition according to procedures described in Duan et al. (2013, 2021). Briefly, gravid female beetles were reared in 1-liter ventilated plastic (oviposition) cups at a density of 3 to 5 females and 3 to 5 males per oviposition cup and provided with fresh tropical ash leaves for egg production. The mouth of the oviposition cup was covered with nylon screen (mesh size = 1 mm^2) and then with a sheet of coffee filter paper (8.25 cm diameter base, Home Life, Eden Prairie, MN, USA) on the top of the screen to serve as oviposition substrate. EAB eggs (F_1) laid (within 48 to 72 h) on the coffee filter paper were counted and incubated in growth chambers (ARB-36L, Percival Scientific Inc., Perry, IA, USA) at 25 ± 1.5 °C with 60% ± 5% relative humidity (RH) and a photoperiod of 16:8 (L: D) hours for 7 days prior to use for rearing larvae with ash bolts for the study.

To produce mature EAB larvae for the experiment, we inoculated bolts of tropical ash (20 cm in height × 2.5 to 3.5 cm in diameter) or green ash (20 cm in height × 6.0 to 6.8 cm in diameter) with 7-day-old EAB eggs (6 to 8 eggs per bolt). Eggs were held in place with parafilm that was wrapped around the circumference of the bolts. Following egg inoculation, the bottoms of bolts were inserted 2.5 cm into floral foam bricks (OASIS, Smithers-Oasis Company, Kent, OH, USA) saturated with distilled water and a 0.1% solution of methyl paraben (to prevent fungus mold) and placed in clear screen-covered crisper boxes (58.4 × 41.3 × 31.4 cm, Sterilite Corporation, Townsend, MA, USA). The rearing boxes were then incubated in an environmental chamber at 30 ± 0.5 °C, 65% ± 10% RH, and a photoperiod of 16:8 (L: D) h for 12 weeks to allow EAB larvae to

reach the mature J-larval stage, which would have entered obligatory diapause (Duan et al. 2021).

Temperature Treatments

We randomly assigned each EAB-infested bolt containing J-larvae to one of nine temperature treatments: 1.7, 4.4, 7.2, 10.0, 12.8, 15.6, 18.3, 21.1, and 23.9 °C. Refrigerators (TSG205SA, Thermos Fisher Scientific Waltham, MA, USA) were used to conduct the 1.7 to 7.2 °C treatments, and the 10.0 to 23.9 °C treatments were conducted in reach-in environmental chambers (Percival LT-36VL or AR-66L, Perry, Iowa). The temperature error specification for all refrigerators and growth chambers used in the study was ±0.5 °C and the temperature inside each refrigerator or growth chamber was monitored with a HOBO datalogger (UX1000-011A, Onset Computer Cooperation, Bourne, MA, USA) throughout the study period. Each temperature treatment was replicated at 6 different times—3× with *F. uhdei* bolts and 3× with *F. pennsylvanica* bolts between December 2021 and June 2023. After 90 days in their respective temperature treatment, bolts were removed from each temperature treatment, placed individually in rearing containers and held at 27 °C (±0.5 °C) for adult emergence. Adult emergence was monitored and recorded daily. Adult development and emergence does not proceed until after mature J-larvae successfully terminate diapause, which requires exposure to appropriate chill temperatures for approximately 90 days (Duan et al. 2021). Thus, diapause termination of mature EAB J-larvae that had been exposed to appropriate low temperatures was confirmed by adult emergence.

After approximately six weeks at 27 °C when adult emergence had stopped, all bolts were dissected and the life stage and fate (ie, dead J-larva, live J-larva, dead adult, or emerged adult) of all larvae were recorded. In total, we obtained 372 viable mature J-larvae (217 from green ash and 115 from tropical ash) for the experiment, corresponding to 37 to 46 larvae per temperature treatment.

Data Analysis

Although each temperature treatment was replicated 3× with *F. uhdei* bolts and 3× with *F. pennsylvanica* bolts at different times, we did not include host species as a factor in our analysis because we have no plausible reason to expect host tree species to influence diapause termination or mortality (Duan et al. 2013). For analyses, we pooled all EAB reared or dissected from all bolts within each replicate.

We modeled the probability of adult emergence (p) using a generalized linear model (GLM) with binomial errors and a logit link [Logit (p) = $\beta_0 + \beta_1 T + \beta_2 T^2$], including linear ($\beta_1$) and quadratic ($\beta_1$) effects of temperature (T) to account for the non-monotonic relationship between temperature and adult emergence or diapause termination (DT). This logit model was selected due to the limited number of temperature treatments, which precluded fitting more parameter-rich nonlinear thermal performance models. Inverse predictions of optimal temperature range were conducted using logit scale for 50% and 90% of the population successfully terminating their diapause or emerging to adult beetles (designated as DT_{50} and DT_{90}, respectively).

For temperature treatments that resulted in successful diapause termination (ie, adult emergence) under the warm rearing temperature (27 °C), we analyzed post diapause development time for adult emergence using a generalized linear mixed effect model (GLMM) with temperature treatment being the fixed effect and replicate the random effect, and a Gaussian distribution. In addition, we analyzed the mortality of mature EAB larvae exposed to different temperatures using the generalized regression platform with a binomial distribution with replicates (bolts) as the random effect. All statistical procedures were conducted with RStudio (RStudio Team 2022) or JMP Pro 18.2.2 (SAS 2025).

Results

Adult emergence occurred from EAB-infested bolts chilled at temperatures between 7.2 and 15.6 °C, indicating successful completion or termination of larval diapause within this range. No adults emerged from EAB-infested bolts chilled at the temperature ≤2.1 or ≥18.3 °C. The proportion that successfully completed diapause (ie, resulting in adult emergence) increased from 68.4% at 7.2 °C to 100% at 10.0 °C but decreased from 97.5% at 12.8 °C to 37.3% at 15.6 °C. Both linear and quadratic effects of the temperature (T) on the proportion of diapause termination were significant (Logit GLM model AIC ≈ 17; $\beta_1 = 6.19596$, Z-value = 4.215, $P < 0.0001$; $\beta_2 = -0.2789379$, Z-value = −4.324, $P < 0.000$), and the predicted low to high temperatures for DT_{50} were 6.9 °C and 15.3 °C, and for DT_{90} 7.9 °C and 14.3 °C, respectively (Fig. 1).

For the temperatures between 7.2 and 15.6 °C that resulted in successful adult emergence, the median time for post diapause development to adults (ie, adult emergence time) at the rearing temperature (27 °C) ranged from 23.9 to 26.9 days (Table 1). Chill treatment significantly affected the mean number of days required for post diapause development to adult emergence ($F = 5.515$, df = 1, 70; $P = 0.0217$), with the number of days required for adult emergence increasing as chill temperature increased (Table 1).

Data from the bolt dissections at the end of the experiment (Fig. 2) showed that the proportion of mature EAB larvae that died before completing diapause and emerging as adults differed significantly among chill temperatures ($F = 4.70$, df = 8, 45, $P < 0.0003$). Mortality was lower for temperatures between 1.7 and 12.8 °C (0% to 7.1%) compared to temperatures between 18.3 and 23.9 °C (16% to 32.6%) (Fig. 2).

Discussion

Results from our study demonstrated that mature EAB J-larvae were able to complete diapause when exposed to temperatures between 7.2 and 15.6 °C for 90 days. After diapause termination, the duration of post diapause development to adults (ie, adult emergence) at warm rearing conditions (27 °C) differed among chill treatments, with development time generally increasing as chill temperature increased. In addition, the proportion of mature EAB larvae that died before completing diapause development to adults was lower for temperatures between 1.7 and 12.8 °C (0% to 7.1%) compared to 15.3 to 23.9 °C (16% to 32.6%). These findings indicate that temperatures experienced during diapause significantly affect EAB diapause termination, post diapause development, and survival of diapausing larvae.

The narrow range of temperatures in which mature EAB larvae can complete diapause may lead to significant spatiotemporal variation in EAB phenology and distribution. In colder climates

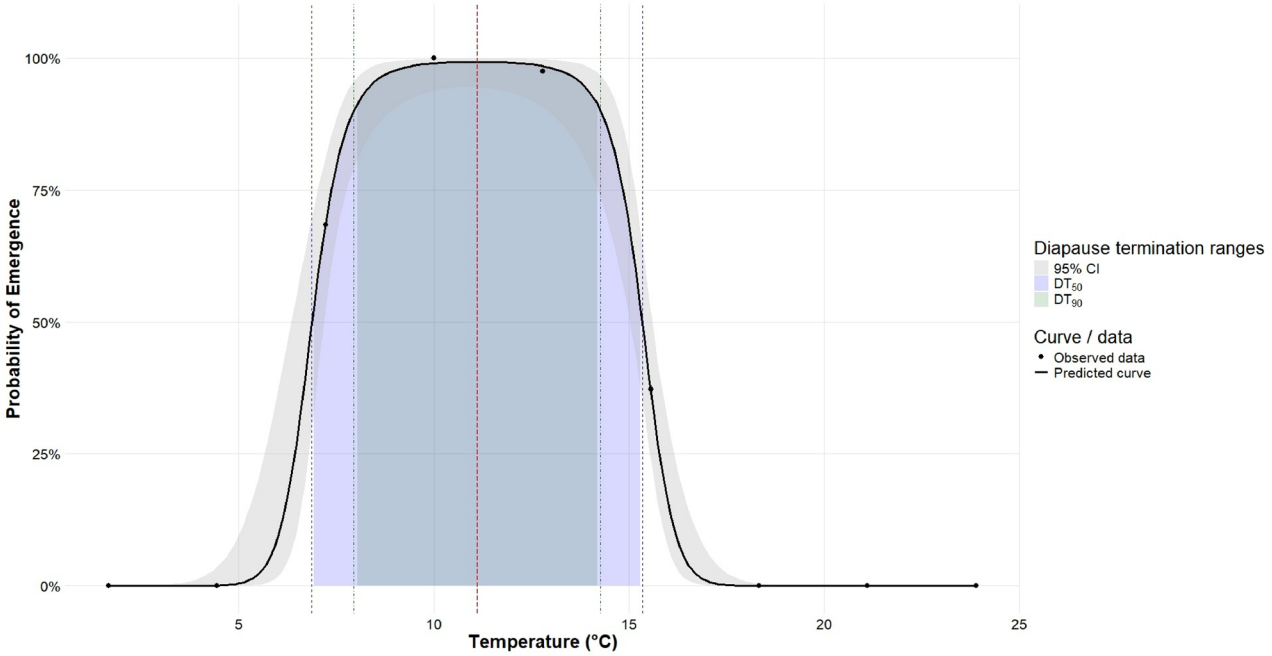

Fig. 1. Temperature-dependent responses in EAB diapause termination (DT) or adult emergence as modeled by a generalized linear model (GLM) with binomial errors and a logit link [Logit (p) = $\beta_0 + \beta_1 T + \beta_2 T^2$], including linear ($\beta_1$) and quadratic ($\beta_1$) effects of temperature (T).

Table 1. Mean (±SE) time for post-diapause development to adults at 27 °C

Temperature treatment for diapause termination (°C)	Total number of adults emerged (*N*)	Mean (±SE) time (day) for adult emergence at 27 °C
4.4	24	23.9 ± 0.7
10	38	24.5 ± 0.5
12.8	38	24.7 ± 0.5
15.6	16	26.9 ± 0.9

Generalized linear mixed model with temperature (as a continuous variable) for fixed effect and replicates (ash bolts) for random effect: $F = 5.515$, df = 1, 70; $P = 0.0217$.

with low winter temperatures, J-larvae would likely meet their diapause requirements during late fall or early winter. In contrast, in warmer climates, these temperature requirements would most likely be met only during the coldest periods of winter. Because winter temperatures in southern regions often remain above the optimal range for successful diapause completion, the minimum number of chill days required for EAB to complete diapause is likely to be longer. Furthermore, inadequate winter temperatures in warmer climates may prevent EAB from completing diapause altogether, potentially limiting its southern range expansion.

Because adult development cannot begin until after diapause has been terminated, winter temperatures will also affect when EAB adults emerge. If diapause requirements have been met, then post-diapause development of J-larvae to adults can begin immediately when temperatures increase above the minimal developmental thresholds. However, if diapause requirements have not been met, development of diapausing J-larvae cannot continue regardless of ambient temperature. This will have cascading effects on oviposition and larval development phenology. For example, the EAB oviposition period will likely be most synchronized in northern climates where most J-larvae have completed diapause before temperatures above developmental thresholds occur the following spring. Depending on when the J-larval stage is reached during the fall and early winter, diapause completion in warmer climates may be less synchronized resulting in some larvae not completing diapause until late winter or early spring. This could result in adult emergence and ultimately oviposition occurring over a longer period. The longer oviposition period would result in more variation in larval size distribution of the current year's generation during the growing season. However, the longer growing season and warmer climates would still allow most of the current generation's larvae to complete development and enter the J-larval stage before winter.

This pattern could have significant implications for the effectiveness of EAB biological control agents. The three Asian larval parasitoids currently being released in North America almost exclusively attack third and fourth instar feeding EAB larvae, leaving smaller larvae and J-larvae not attacked. Because all three parasitoid species are multivoltine, the presence of suitable host stages throughout most of the growing season is critical for their establishment and persistence. In regions where climates allow presence of both semivoltine and univoltine populations, a range of larval instars can be found throughout the growing season, always providing suitable hosts for larval parasitoids. In contrast, in areas where climates only allow univoltine populations, there will be fewer suitable stages available because most will have reached the J-larvae stage before the onset of winter.

Finally, we highlight that the temperature-dependent response of EAB diapause termination in our study displayed an inverted U- or "flat-topped" shape. Sharp thresholds occurred at both low (DT_{50} = 6.9 °C) and high (DT_{50} = 15.3 °C) temperatures, with diapause termination remaining relatively invariable between the low and high DT_{90} values (7.9 °C and 14.3 °C, respectively). This pattern suggests that temperature may exert a nominal effect on diapause termination in EAB J-larvae, in contrast to the more continuous or incremental effects typically observed for other life history

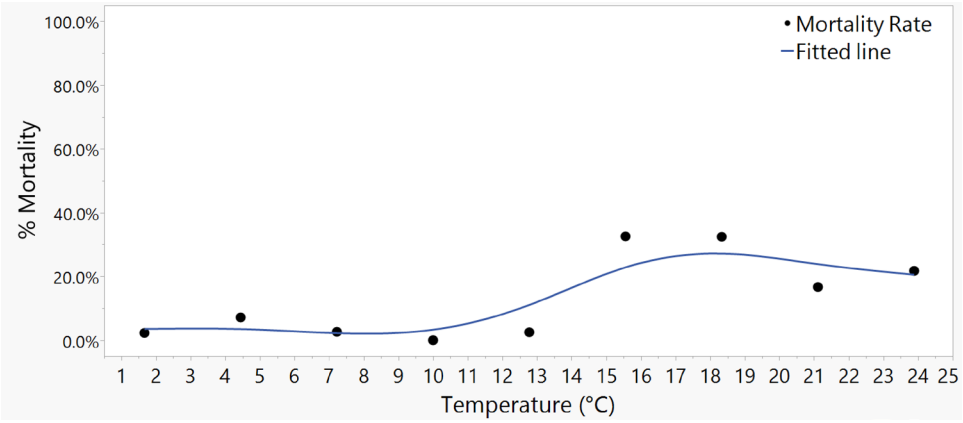

Fig. 2. Mortality of diapaused EAB larvae (J-larvae) in relation to temperature treatments.

traits (eg, fecundity and development time, locomotion) that are unimodal and often left-skewed (Angilletta 2009, Kontopoulos et al. 2024, von Schmalensee et al. 2024). This inverted U-shaped temperature response of EAB diapause termination has been observed in studies of temperature effects on survivorship of many other insects (eg, Amarasekare and Sifuentes 2012); however, the underlying physiological and molecular mechanisms are still largely unknown (Van der Have 2002, Denlinger 2022). Future studies should focus on the underlying physiological and molecular mechanisms for the normal effect of temperature on EAB diapause termination and implications of such effects on the EAB geographic distribution limit in both warm and cold climate conditions.

Author Contributions

Jian J. Duan (Conceptualization [lead], Data curation [equal], Formal analysis [lead], Methodology [lead], Project administration [lead], Resources [lead], Supervision [lead], Writing—original draft [lead], Writing—review & editing [equal]), Toby R. Petrice (Formal analysis [equal], Resources [equal], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Jonathan M. Schmude (Data curation [lead], Investigation [lead], Methodology [equal], Validation [equal], Visualization [equal], Writing—review & editing [equal]), and Tyler Hagerty (Formal analysis [equal], Validation [equal], Visualization [equal], Writing—review & editing [equal])

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Conflicts of Interest

The authors have no conflict of interests to declare.

Data Availability

Data will be available upon request and will also be deposited to the USDA Data repository (Ag Data Commons) at a later time.

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