Received: 26 June 2024 | Accepted: 24 July 2024

DOI: 10.1002/ecs2.70028

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Agroecosystems

Heat wave impacts on crop-pest dynamics are dependent upon insect ontogeny and plant resistance

Nalleli Carvajal Acosta[1,2,3] | **Luke N. Zehr**[2] | **Joshua S. Snook**[2,4] | **Zsofia Szendrei**[3,4] | **Michael Kalwajtys**[2] | **William C. Wetzel**[1,2,3,5]

[1]Land Resources & Environmental Sciences, Montana State University, Bozeman, Montana, USA

[2]Department of Entomology, Michigan State University, East Lansing, Michigan, USA

[3]Kellogg Biological Station, Hickory Corners, Michigan, USA

[4]Entomology Department, Louisiana State University, Baton Rouge, Louisiana, USA

[5]Department of Integrative Biology, Michigan State University, East Lansing, Michigan, USA

Correspondence
William C. Wetzel
Email: william.wetzel@montana.edu

Funding information
USDA National Institute of Food and Agriculture, Grant/Award Number: 2020-67013-31919

Handling Editor: John M. Humphreys

Abstract

Heat waves, brief periods of unusually high temperatures, are damaging to agroecosystems and are increasing in frequency and intensity due to climate change. Despite growing appreciation for the threat that heat waves pose to agricultural sustainability, we have a poor understanding of what determines their impact on agroecological interactions in the field. Here, we report the results of a field experiment that examined how heat waves and their timing interact with crop pest resistance to influence the interactions between potato (*Solanum tuberosum*) and its most damaging pest, the Colorado potato beetle (CPB; *Leptinotarsa decemlineata*). We used open-top chambers and ceramic heaters to generate heat wave conditions in field plots with pest-resistant and pest-susceptible potato varieties at four CPB developmental stages. We then assessed CPB performance, leaf herbivory, and tuber yield. The neonate-stage heat wave reduced larval survival by 10%, but the surviving larvae were 18% larger and developed 15% faster. However, these effects occurred only on the susceptible variety; both larval survival and growth were unaffected by the heat wave in the pest-resistant variety. Moreover, the neonate-stage heat wave reduced adult survival by 15%, suggesting negative carry-over effects of early-life heat exposure. Heat wave events after the neonate stage had no effects on CPB performance, crop damage, or tuber yield. Our results indicate that timing and pest resistance in crops are essential for understanding the impacts of extreme heat events on crop-pest dynamics. Agroecological pest management in an increasingly variable and extreme climate will likely benefit from the development of strategies that account for the seasonal timing of potential heat events and from the continued use of crop varieties bred for pest resistance, which our results suggest may dampen the impacts of extreme temperatures on crop-pest interactions.

KEYWORDS
carry-over effects, climate change, Colorado potato beetle, extreme weather, *Leptinotarsa decemlineata*, pest management, plant resistance, *Solanum tuberosum*, thermal stress

INTRODUCTION

A major goal in agroecology is learning how to manage agroecosystems sustainably in the face of a changing climate. Although most climate change research has focused on the consequences of gradual changes in climate means, a growing number of studies suggest that a large component of the effect of climate change on agriculture and conservation is due to the increase in the frequency and intensity of extreme climate events (Easterling et al., 2000; Lesk et al., 2016; Maxwell et al., 2019; Meehl & Tebaldi, 2004). For example, heat waves, brief periods of stressfully high temperatures (Robinson, 2001), have been estimated to have reduced crop yield by almost 10% over the last 60 years with the severity of impacts tripling from the mid-20th century to the present (Brás et al., 2021; Lesk et al., 2016; Miller et al., 2021). Although large-scale studies have highlighted the challenge that heat waves pose for global agricultural sustainability, we have a much poorer understanding of how heat waves impact interactions between pests and crop plants at the field scale. Ensuring the resilience of ecologically based management strategies that rely on biological processes (Lewis et al., 1997) requires a deeper fundamental understanding of how heat waves alter the interactions between crop plants and their pests.

An important barrier to our ability to understand and predict the effects of a heat wave on crop-pest interactions is heat wave timing. Heat waves can impact a system at any time during a growing season, and important pests, such as insects, often have complex life cycles with varying physiological tolerances between stages of metamorphosis. A result of this is that the heat sensitivity of pests may vary across ontogenetic stages, leading heat waves to have different ecological impacts at different times during the growing season (Cinto Mejía & Wetzel, 2023; Lowe et al., 2021). Although lab studies have well established that thermal tolerance can differ between insect stages (Chen et al., 2018; Kingsolver & Buckley, 2020; Klockmann et al., 2017; Sales et al., 2021; Vasudeva, 2023), little is known about how the timing of heat impacts insect pests as they interact with their host plants in the field. Field studies that impose heat wave conditions at different times during crop and pest development would directly inform our understanding of how heat wave timing impacts crop-pest interactions and our ability to manage them.

A second gap in our understanding of how heat waves influence crop-pest interactions is whether these events will impact the efficacy of traits that confer pest resistance to crop plants. Indeed, the employment of pest-resistant crop varieties is a cornerstone of ecological pest management, making it essential that we identify the resilience of pest-resistant crops. Recent heat wave studies in natural systems have found that even short bursts of heat can reduce plant chemical defenses (Cope et al., 2023; Harvey et al., 2020; Veteli et al., 2002), whereas laboratory evidence suggests that high levels of chemical resistance may magnify the negative effects of heat waves on herbivores with such effects varying with insect ontogeny (Yang et al., 1996). However, studies investigating the combined effect of heat stress and plant resistance (including physical defenses) in agricultural field settings are lacking. Moreover, field studies with interacting plants and insects are needed to reveal how the impacts of heat waves on plant resistance feedback to impact plant growth, performance, and yield.

A final key gap in our understanding of how heat waves impact agroecology is the degree to which brief events can have lasting consequences via carry-over effects. For example, the effects of thermal stress during early life stages may carry through ontogeny to impact adult biology with potential consequences for population dynamics (i.e., pest outbreaks or population breakdowns) (Harvey et al., 2020; Shinner et al., 2020; Vasudeva, 2023). Larval heat exposure can negatively impact adult size (Kingsolver & Huey, 2008) and reproduction (Bader & Williams, 2012; Forster et al., 2011; Hodin & Riddiford, 2000). Additionally, heat stress during metamorphosis has been shown to damage developing reproductive structures and thereby reduce adult reproductive success (Steven, 2004). For example, brief exposure of diamondback moth larvae to 40°C reduced adult reproduction, with stronger effects when heat stress was experienced closer to adulthood (Zhang et al., 2015). However, carry-over effects of thermal stress do not always occur (see Potter et al., 2011; Xing et al., 2014), potentially because their effects may be influenced by other factors. For example, host-plant quality and herbivore resistance may make it more difficult for herbivores to recover from heat stress and exaggerate carry-over effects. Additionally, past studies have been lab based, making the importance of carry-over effects in the field a key knowledge gap.

Here, we report a field experiment that examined how heat waves and their timing interact with crop pest resistance to influence the interactions between potato (*Solanum tuberosum*) and its most damaging pest, the Colorado potato beetle (CPB; *Leptinotarsa decemlineata*). We used open-top chambers and ceramic heaters to generate heat wave conditions in field plots with a pest-resistant and a pest-susceptible potato variety at different CPB developmental stages. We asked: (1) Are the effects of heat waves on insect pest performance dependent on the herbivore's ontogenetic stage? Based on studies in similar organisms (Chen et al., 2018), we predict that heat waves occurring during earlier ontogenetic stages will have stronger effects on CPB performance. (2) Do the effects of early-life heat exposure carry over to adulthood? Given that negative carry-over effects appear to be common in insects, we predict that larval heat exposure will negatively affect adult fitness. (3) Are heat wave effects on insect performance influenced by pest resistance? We hypothesize stronger negative effects of heat stress in the crop-resistance variety due to the negative compounding effects of low food quality and thermal stress. Finally, (4) what are the consequences of heat waves for plant herbivory and crop yield and are these influenced by pest-resistant crops? Because most herbivore damage occurs during the CPB larval stage and this is also the stage when we predict that insects will be more heat sensitive, we expect higher herbivory levels and stronger effects on crop yield during earlier heat wave events, but these effects may be weaker in the pest-resistant variety. Developing a foundational understanding of how heat wave timing affects insect pests and consequently crop damage and yield would allow farmers to make informed decisions about the most appropriate ecological management strategies (i.e., release of natural enemies, pest-resistant crops) under heat wave conditions and patterns of extreme weather in their region.

MATERIALS AND METHODS

Study system

Potato (*S. tuberosum* L.) is among the most important crops worldwide. Potato plants produce glycoalkaloids as defensive chemicals against herbivores (Hlywka et al., 1994). However, domesticated varieties are less chemically defended than wild varieties, making them more susceptible to pests. Breeding programs have produced several resistant varieties through crosses with wild species (Flanders et al., 1992). One of these is King Harry, a hybrid between the wild species *Solanum berthaultii* and *S. tuberosum*, with high densities of glandular trichomes (Kowalski et al., 1992; Neal et al., 1989; Tingey & Sinden, 1982). The leaf surface of *S. berthaultii* hybrids is covered by glandular trichomes, which impair insect movement and feeding. This trait confers natural deterrence to insect pests, making them more resistant than the Atlantic variety, one of the most popular commercial varieties.

CPB is the main insect pest in potato fields, causing significant damage to crops and severely reducing tuber yield (Radcliffe, 1982). The life cycle of CPB consists of an egg stage, four larval stages, a pupal stage, and an adult stage. The duration of a complete cycle varies greatly according to temperature (Ferro et al., 1985). In northern climates, CPB adults spend the winter 12–25 cm underground. Overwintering adults emerge in the spring and disperse to a suitable host plant where they begin to mate and lay eggs (Boiteau et al., 2003). Fourth instar larvae pupate in the soil, and adults begin to emerge after 5–10 days (Hare, 1990). In northern regions, a single generation reproduces throughout the growing season, whereas southern populations may produce more than one generation per year. Adults and larvae feed on potato leaves and other tissues, but the most damage occurs during the latest larval stages when CPB damage can cause complete defoliation (Alyokhin et al., 2008). In addition to traditional pest management practices, such as insecticides and biocontrol, incorporating CPB-resistant potato varieties has proven to be an effective management tool (Maharijaya & Vosman, 2015).

Experimental design

To assess the effect of heat wave timing and crop resistance on the interactions between CPB and potato plants, we conducted a field experiment at the Michigan State University Kellogg Biological Station (Hickory Corners, MI) during the 2021 growing season. We planted seed potatoes within 1-m^2 plots from Atlantic, a pest-susceptible variety, and King Harry, a pest-resistant variety. We planted four plants within each plot, all from the same variety, resulting in 130 plots (65 per variety), totaling 520 plants. When plants began sprouting and before naturally occurring CPB populations arrived, we covered the plots with 1 m^2 by 80 cm tall mesh cages (Lumite, Inc., Georgia). The sides of the cages were buried 15 cm below the soil surface to prevent arthropod movement among plots.

When the plants were about 10 days old, we placed CPB egg masses of approximately 40 eggs into each cage. Egg masses were gathered from a CPB colony maintained in rearing cages with adults sourced from Montcalm Research Center, Michigan. Three days later, we surveyed the plots to ensure that each had 40 neonates, moving larvae among plots (but not between varieties) to even out the number.

To investigate whether the effects of heat waves are influenced by insect ontogeny, we randomly assigned plots from each potato variety to four different heat wave timings or a control with ambient temperatures ($n = 13$ per heat wave timing × potato variety treatment combination). Each heat wave treatment was a single 4-day heat wave applied at different times during the 2021 growing season: June 22–26, June 30–July 4, July 9–13, and July 19–23. Each heat wave corresponded to different stages of CPB development, with the first heat wave occurring during the neonate stage, the second during later larval stages, the third during pupation, and the fourth during adult emergence.

Based on climate records, we simulated historically extreme heat wave events using an electric 300-W ceramic heater (Tempco, Illinois) hung in the opening of a pyramidal open-top chamber with a wood frame and anticondensate greenhouse plastic sides (6 mil, 91% light transmittance, Poly-Ag, California). This system increased temperatures by an average of ~4°C during the day and ~2°C at night, achieving day and night temperatures of 28 ± 4.1°C (mean ± SE) and 19 ± 2.5°C in the heat wave treatments compared with 24 ± 2.9°C and 17 ± 2.6°C in controls (Appendix S1: Figure S1). To prevent a heat shock in plants and insects, we initiated the heat wave during the night when temperatures were cooler. Control plots were covered with a dummy chamber consisting of an identical wooden structure but covered with a breathable mesh material. At the end of each heat treatment, we removed the heaters and chambers but left the cages in place.

After each of the first two heat waves (the neonate- and larval-stage heat waves), we recorded the larval count, length, and instar stage to assess larval survival, growth, and development. When the first adults began to emerge, which corresponded with the end of the third heat wave, we surveyed plots every other day for six consecutive weeks and collected and recorded the number of adult beetles emerged. Adult beetles were frozen immediately after collection, oven-dried, weighed, and sexed. We estimated leaf herbivory after the second heat wave event to assess the effects of heat wave timing and plant resistance on leaf damage. Percent herbivory across the whole plant was estimated visually following the Primary HerbVar Survey Protocol (Wetzel et al., 2023). At this time, most larvae had pupated, thus allowing us to estimate total herbivory by larvae, when most plant tissue is consumed. In the fall, when plants began senescing aboveground, we dug tubers from each plant, sorted them by plot into size and quality classes, and measured the mass of marketable tubers (USDA Agricultural Marketing Service, 2011). See Figure 1 for details on experiment timeline and data collection.

Statistical analysis

Effect of heat wave timing on CPB fitness

Because of our inability to measure pupae while they were in the soil, we did not measure CPB performance right after the second and third heat waves when large parts of the population were pupating. For larval performance, we assessed only the effects of a neonate-stage heat wave as most larvae began pupating after the second heat wave (Appendix S1: Figure S2). Similarly, we did not assess the effects of the third heat wave (corresponding to the pupa stage) on pupa performance. Thus, the remainder of the CPB performance analyses pertain to the adult stage.

Larval performance

We assessed the effects of a neonate-stage heat wave and plant resistance on larval performance: survival, growth,

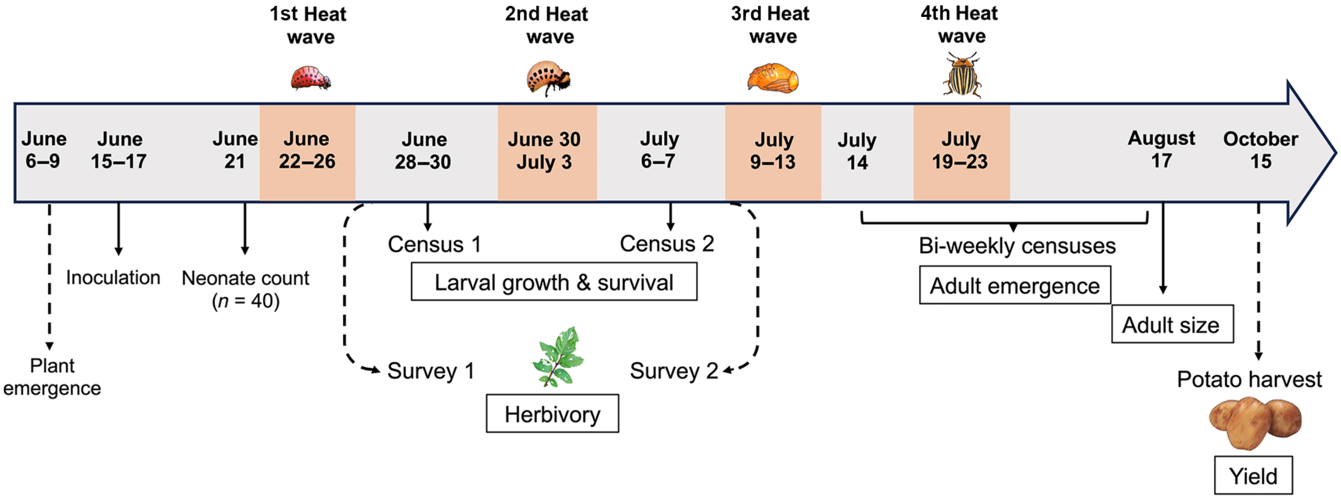

FIGURE 1 Timeline of experiment and data collection information. The heat wave period is indicated by light orange. Data collection is indicated by solid arrows for insects and by dashed arrows for plants. Plant and insect performance measures are shown within boxes. Adult size was determined over a 6-month period beginning at the end of Colorado potato beetle (CPB) adult collection. CPB illustrations by Nalleli Carvajal Acosta.

and development. We used generalized linear mixed models (GLMMs) to investigate the effect of a neonate-stage heat wave on larval survival, growth (larval length in millimeters), and instar development (as indicated by the instar stage). For the larval survival model, we used a GLMM with a Poisson error distribution and the number of larvae surviving as the response variable. For the larval development model, we modeled whether or not the observed larvae had reached the third larval instar at the time of measurement, with second and third instar as the binomial response variable. For larval growth, we used linear mixed models (LMMs) for overall larval growth and larval growth within the instar stage by adding instar stage as a covariate.

Adult performance

We further investigated whether heat wave timing and plant resistance affect CPB developmental rate to adulthood, adult mass, and survival. To do so, we used an LMM for developmental rate and a covariate LMM with sex as the covariate term for adult mass. The developmental rate was estimated by log transforming the rate of emergence (1/days to emergence). Finally, we analyzed adult survival using a GLMM with a Poisson error distribution and the number of surviving larvae as the response variable.

All mixed models included heat wave treatment, plant variety, and their interaction as fixed effects, and plot as a random effect, and were implemented in the lme4 package (Bates et al., 2015) in R V. 4.2.1 (R Core Team, 2018). We performed Tukey's tests for pairwise differences between treatment levels in the emmeans package (Lenth, 2023).

Effect of heat wave timing on plant herbivory and potato yield

We analyzed the effects of the two heat waves applied during the CPB larval stage (first and second) and whether they interact with plant resistance to determine the proportion of leaf tissue damaged by CPB larvae. We used a zero-inflated beta-regression model with heat wave treatment and plant resistance and their interactions as fixed effects and plot as a random effect in the glmmTMB package (Brooks et al., 2017). Overall tuber mass and marketable yield were analyzed using linear regression models. We performed Tukey's tests for pairwise differences between treatment levels as described above.

RESULTS

Effect of heat wave timing and crop resistance on CPB performance

Larval stage

We detected strong but contrasting effects of the neonate-stage heat wave on larval survival and growth. A significantly lower number of larvae survived the heat wave (32.5%, 13 count) than those in the control (42.5%, 17 count) ($\chi^2 = 4$; df = 1; $p = 0.045$; Figure 2A). In contrast, the heat wave increased the size of the surviving larvae, both overall by 1.2 mm ($F_{1,127} = 23.5$; $p < 0.001$; Figure 2C), and within instar stage by 0.5 mm in the second instar and 0.8 mm in the third instar stage ($F_{1,127} = 13.7$; $p = 0.001$; Figure 2E). Larvae also grew faster under the heat wave event, with 15% more larvae reaching the third instar compared with the control treatment at the time of measurement ($\chi^2 = 9.9$; df = 1; $p = 0.001$; Appendix S1: Figure S3). We detected no interactive effect of heat wave and variety on larval survival ($\chi^2 = 2$; df = 1; $p = 0.153$). However, Tukey's test revealed that more larvae survived in the pest-susceptible variety under control conditions compared with other treatment combinations ($p < 0.05$), whereas survival remained comparable among all other treatment combinations (Figure 2B). We detected an interactive effect between the heat wave treatment and variety on larval growth ($F_{1,127} = 8.6$; $p = 0.003$; Figure 2D). Tukey's test shows that larvae feeding on the pest-susceptible variety under a heat wave event grew larger than any other treatment combinations ($p < 0.001$). In contrast, we detected no significant differences in larval growth between the heat wave and control groups when feeding on the pest-resistant variety ($p = 0.98$; Figure 2D). Across both the control and neonate-stage heat wave treatments, the pest-resistant variety had strong negative effects on all measures of larval performance, with fewer larvae surviving in the pest-resistant variety (King Harry = 15 vs. Atlantic = 21) ($\chi^2 = 13.5$; df = 1; $p = 0.002$; Appendix S1: Figure S4) and supporting overall smaller larvae (~0.7 mm smaller on average) ($F_{1,127} = 26.5$; $p < 0.0001$; Appendix S1: Figure S4).

Adult stage

We found no significant differences in adult survival ($\chi^2 = 1.6$; df = 3; $p = 0.64$), mass ($F_{4,78} = 0.11$; $p = 0.98$), or CPB developmental rates to adulthood ($F_{3,119} = 0.15$; $p = 0.92$), among the control and the heat wave events (Figure 3). However, because we had previously detected

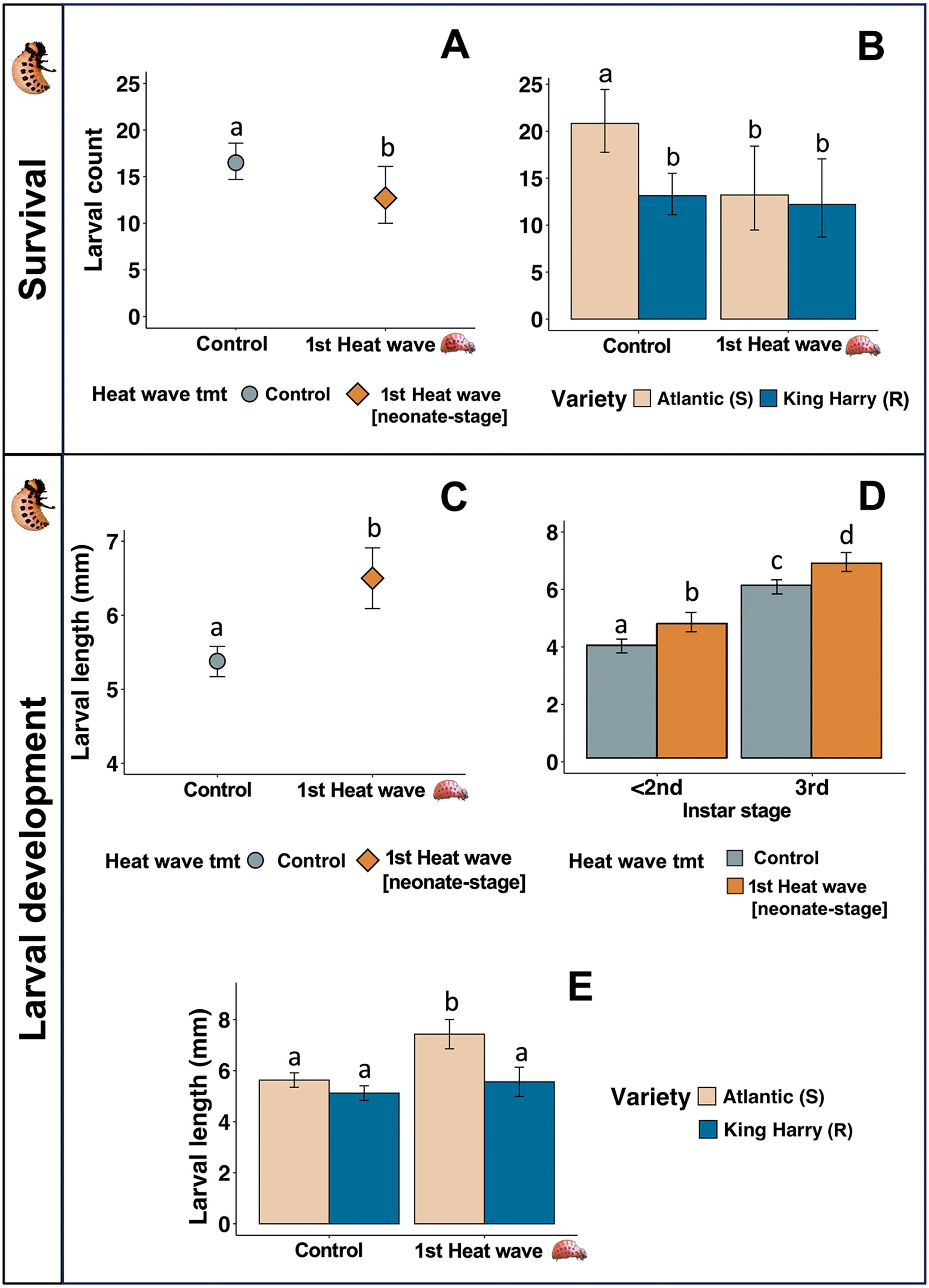

FIGURE 2 Legend on next page.

such a strong larval response to the neonate-stage heat wave, we conducted follow-up analyses comparing adult performance only in the control and neonate-stage heat wave groups. We found that a neonate-stage heat wave significantly reduced adult survival by 22% ($\chi^2 = 6.2$; df $= 1$; $p = 0.02$) but detected no significant differences in adult mass ($F_{1,32} = 0.02$; $p = 0.88$) or developmental rates ($F_{1,72} = 0.38$; $p = 0.54$). No interactive effects of variety and heat wave treatments on any measure of adult performance were detected. Potato variety had weak effects on adult survival ($\chi^2 = 3.7$; df $= 4$; $p = 0.05$), which was lower in the pest-resistant variety (King Harry = 11, Atlantic = 13, on average), but not on adult mass ($F_{1,83} = 4.6$; $p = 0.42$).

Effect of heat wave timing on plant herbivory and potato yield

Herbivory was lower in the first heat wave treatment (2.18%) in comparison with that in the control (3.26%) and second heat wave (3.55%), but these trends were marginally significant ($\chi^2 = 4.9$; df $= 2$; $p = 0.08$; Figure 4A). We detected a marginally significant interactive effect of variety and heat wave treatments ($\chi^2 = 5.4$; df $= 2$; $p = 0.06$) with higher herbivory in the pest-susceptible variety under control conditions than in other treatment combinations (Figure 4B). We also observed lower herbivory in the pest-resistant variety across heat wave treatments, suggesting that plant resistance was maintained under the heat wave events (Figure 4B). Potato variety had strong effects on leaf herbivory ($\chi^2 = 11.9$; df $= 1$; $p = 0.0005$) as lower herbivory was observed in the pest-resistant variety (2.26%) than in the pest-susceptible variety (3.93%) (Appendix S1: Figure S4). Finally, heat wave timing had no significant effects on total tuber mass ($F = 0.89$; df $= 4$; $p = 0.46$) or marketable yield ($F = 0.77$; df $= 4$; $p = 0.54$).

DISCUSSION

In this study, we examined the effects of heat wave timing and crop resistance on the performance of an economically important pest, the CPB. We showed that the timing of a heat wave event determines the pest response and that crop resistance remains effective as a management strategy under a heat wave event. A heat wave occurring during the neonate stage, but not during later ontogenetic stages, strongly affects herbivore performance. These effects, however, opposed each other on distinct measures of larval performance, with heat stress negatively affecting larval survival and positively affecting larval growth. Both effects were stronger for larvae on the pest-susceptible variety, whereas larval performance was unaffected by the heat wave on the pest-resistant variety. Despite the many organismal level effects, we found no changes in herbivory or yield, possibly due to the contrasting heat wave effect on insect performance. Altogether, these results show that accounting for the timing of a heat wave event, the insect ontogenetic stage, and plant resistance are important for predicting heat wave impacts on crop-pest dynamics and understanding their consequences for crop yield.

Heat wave timing matters

We hypothesized that CPB would be more affected by heat stress during earlier ontogenetic stages. Indeed, a heat wave applied during the neonate stage had strong effects on larval survival and growth, unlike subsequent heat waves. A plausible explanation for high neonate mortality under heat wave conditions is desiccation due to evaporative cooling (Neven, 2000). Evaporative cooling is a common mechanism to prevent overheating whereby insects release heat by exuding water from either body storages or water obtained from plants (Prange & Pinshow, 1994). There is a lower body size limit at which evaporative water loss becomes ineffective (Prange, 1996), as insects with a smaller body size have lower water storages as well as larger surface to body size ratios from where water can be lost. Thus, it is likely that at the neonate stage, when insects are smaller, larvae are more likely to die from heat-induced desiccation due to depletion of limited body water storages coupled with their larger surface-size ratios.

Besides morphological differences, behavioral thermoregulation (i.e., microhabitat selection) may also be an important factor explaining ontogenetic differences in

FIGURE 2 Effects of a neonate-stage heat wave and crop resistance on larval performance. (A) The main effect of a neonate-stage heat wave on larval survival. (B) The interactive effect of a neonate-stage heat wave with plant resistance, where (S) indicates a susceptible variety and (R) a resistant variety. (C–E) The main effect of a neonate-stage heat wave on larval growth, (C) overall and (D) within the instar stage; (E) the interactive effect of a heat wave and crop resistance, indicated by (S), susceptible, and (R), resistant. Bars with different letters are significantly different ($p < 0.05$). Each point or bar represents model estimates for larval count or length, and error bars indicate 95% CIs. Colorado potato beetle larvae illustration by Nalleli Carvajal Acosta. tmt, treatment.

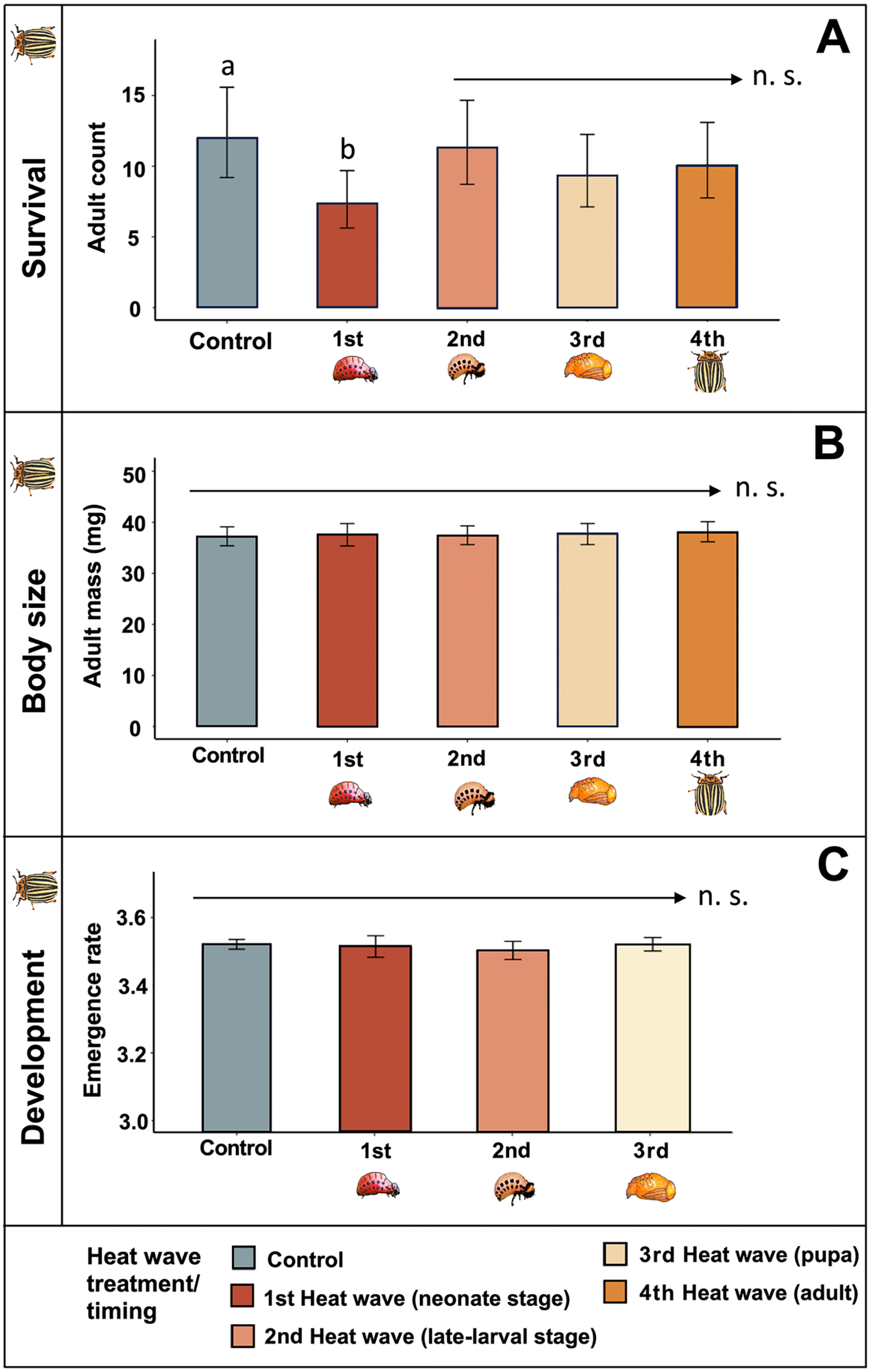

FIGURE 3 Carry-over effects of heat wave treatment and timing on adult performance. (A, B) The effects of four heat wave timings on adult survival and mass, respectively. (C) The effects of the first three heat wave events on emergence rates calculated as log(1/days to emergence). Different letters indicate significant differences ($p < 0.05$), and "n. s." indicates nonsignificant differences among groups. Significance codes in (A) are based on analysis between control and first heat wave groups. Each bar represents model estimates for averages of adult count, body mass, and developmental rates, respectively. Error bars indicate 95% CIs. Adult Colorado potato beetle illustration by Nalleli Carvajal Acosta.

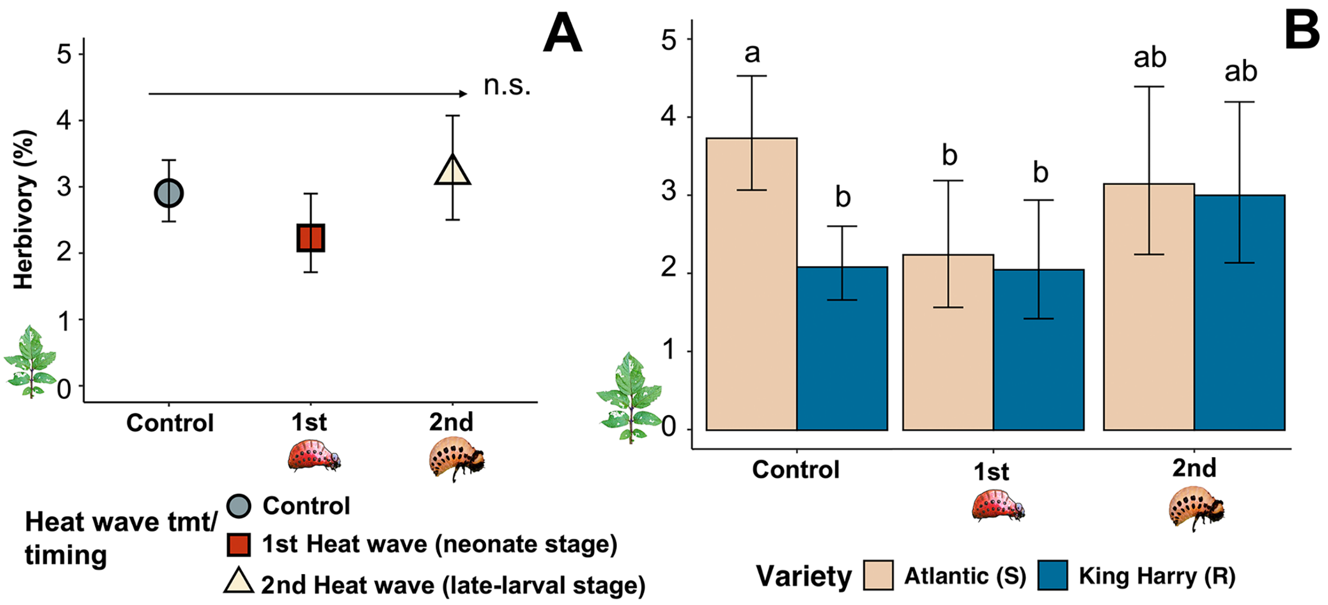

FIGURE 4 Effects of larval-stage heat waves on plant herbivory. (A) The main effects of the heat waves on percent herbivory. (B) The interactive effect of heat waves and crop resistance on percent herbivory, where (S) indicates susceptible and (R) resistant variety. Different letters indicate significant differences ($p < 0.05$), and "n. s." indicates nonsignificant differences among groups. Each point or bar represents model estimates for average percent herbivory. Error bars indicate 95% CIs. Potato leaflet illustration by Nalleli Carvajal Acosta. tmt, treatment.

heat tolerance (Bodlah et al., 2023; Klockmann et al., 2017; Nielsen & Papaj, 2015). For instance, less mobile stages such as egg and pupa should have lower heat tolerance because of a lack of alternative behavioral options. In contrast, we observed that the immobile pupa stage was no more susceptible to heat stress than mobile larval stages. We believe this might be due to CPB pupae dwelling in the soil where they experience thermal regimes buffered by the denser soil environment, allowing them to escape the full effects of increasing aboveground temperatures (Bale et al., 2002).

In contrast to larval survival, a neonate-stage heat wave positively affected larval growth and development. Our results are consistent with several studies showing that warmer temperatures increased food consumption and rates of development in several insect species (Mackey, 1977; Stamp & Bowers, 1990; Van Dievel et al., 2017). Nonetheless, it is unclear whether growth and development are directly affected by temperature. Laboratory evidence suggests that both fitness responses are influenced by different factors, with rates of development being most strongly influenced by temperature, whereas growth, body composition, and reproductive output are greatly affected by nutrition (Clissold & Simpson, 2015). Therefore, the overall insect response to heat stress may be dependent on both temperature and the insect's ability to obtain nutritional plant resources (Iltis et al., 2021).

Our finding shows that a heat wave event occurring during the neonate-stage may significantly alter crop-pest dynamics due to the multiple changes occurring at the organismal level (i.e., increased mortality, accelerated development). Therefore, early heat waves may accelerate pupation and consequently narrow the time window at which insecticides can be applied. Accordingly, growers may benefit from developing a calendar of heat wave vulnerabilities for pest management that allows farmers to predict when in a growing season a heat wave is likely to disrupt, enhance, or have no effect on pest suppression and/or bottom-up processes. For example, based on our field data, an early heat wave accelerates CPB development. A grower could use that information to prepare for an early season heat wave by investing more heavily in top-down control strategies, such as the release of natural enemies.

Heat wave effects on insect pests are dependent on crop variety

We hypothesized that the effects of heat stress would be dependent on plant resistance due to the compounding negative effects of low food quality (higher plant resistance) and thermal stress (Bauerfeind & Fischer, 2013; Iltis et al., 2021). Indeed, we found that heat wave effects were influenced by crop variety, but the trends were in the opposite direction to our predictions. Larval growth was similar in the pest-resistant variety under control and heat wave conditions, suggesting no negative compounding effects of heat wave and pest resistance. Conversely, we found a combined positive effect of lower pest resistance and higher temperatures on larval growth. Among the most likely explanations is that larvae were able to recover from heat stress via compensatory feeding in the pest-susceptible variety, whereas glandular trichomes in the pest-resistant variety may have impeded larval feeding, hampering their recovery (Malakar & Tingey, 2000; Neal et al., 1989). Alternatively, the higher metabolism that occurs at elevated temperatures could have translated to larger body sizes on the higher quality food of the pest-susceptible variety but not the pest-resistant crop variety. These results add to the growing number of studies showing that nutritional availability is key for insects' post-heat recovery (Clissold & Simpson, 2015; Diamond & Kingsolver, 2010; Iltis et al., 2021; Stamp & Bowers, 1990). Moreover, our results underscore the importance of plant resistance traits that impede feeding in mediating insect thermal responses.

Similarly, we detected no negative compounding effects of pest resistance and higher temperatures on larval survival. Larval survival decreased under a heat wave event but only when feeding on the pest-susceptible variety, whereas survival remained consistently low in the pest-resistant variety. This suggests that pest resistance traits and temperature may have independently influenced larval survival. In *S. berthaultii* hybrids, CPB mortality does not appear to be caused by glandular trichome entrapment but rather by starvation, as trichomes limit neonate movement and ability to penetrate the leaf surface (Malakar & Tingey, 2000). Conversely, heat-induced mortality can be the result of multiple physiological processes such as heat shock, protein denaturation, and desiccation, among others (reviewed in Neven, 2000; Williams et al., 2016). It is also possible that differences in thermal tolerance between crop varieties mediate heat wave effects to herbivores. In addition to their defensive function, trichomes are also important for plant thermoregulation (Campitelli et al., 2013; Domanda et al., 2023). Therefore, higher trichome densities in King Harry may confer these plants with higher thermal tolerance, allowing them to maintain homeostasis. Future studies should investigate the role of crop thermal tolerance in mediating heat wave effects on herbivores.

Nonetheless, our results show that the pest-resistant variety remained effective at controlling herbivore attack by consistently reducing larval growth and survival under control and heat wave conditions. These results are encouraging as biological control dependent on higher trophic levels (predators and parasitoids) may not be reliable in a warming climate. Several studies indicate that thermal sensitivity progressively increases with increasing trophic levels (da Silva et al., 2023; Gilbert et al., 2022; Voigt et al., 2003). Top-down control by parasitoids, including those commonly used in potato crops (*Aphidius ervi* and *Macrosiphum euphorbiae*), has been shown to be greatly reduced under high-temperature conditions (Flores-Mejía et al., 2016; Schrevens et al., 2017). Thus, in a future climate with increasingly frequent heat wave events, the employment of pest-resistant crop varieties may continue to be an important and effective pest management tool.

Carry-over effects of early life heat exposure on CPB adult survival

Given the strong larval response to the neonate-stage heat wave, it was surprising that these effects were not carried over to the adult stage. However, our additional analysis showed that a significantly lower number of CPBs exposed to a neonate-stage heat wave survived to adulthood than those under ambient conditions. This was expected as we had previously detected high larval mortality after the first heat wave (neonate stage). However, the neonate-stage heat wave reduced adult survival by an additional 15.5% compared with larval survival (~21.5% adult vs. ~37% larval survival). These results suggest that a neonate-stage heat wave may have lasting effects on CPB fitness, which is consistent with previous studies showing that early-life heat exposure leads to higher adult mortality (Chen et al., 2018; Zhang et al., 2015). In contrast, we found that adult mass and developmental rates to adulthood were unaffected by the heat wave events. It is worth noting that, due to the CPB overwintering behavior in Michigan, we were unable to measure adult reproductive output, one of the adult fitness measures most affected by larval heat exposure (Sales et al., 2021; Vasudeva, 2023). To fully understand heat wave impacts on insect population dynamics, it would be important to explore its effects on adult fertility and reproduction, especially in populations with multiple generations per year.

No heat wave effects on plant herbivory or productivity

In contrast to our hypothesis that larval-stage heat waves will have stronger impacts on plant herbivory and yield, we found no differences in either herbivory or yield among control or heat wave treatments. Our results appear to contradict past studies indicating that higher resource consumption in response to increasing temperatures is most common in agricultural systems (reviewed in Hamann et al., 2021). Compared with diverse natural ecosystems, where insects can feed selectively from hosts, agricultural systems have more restrictive dietary options and less-defended domesticated plants (Whitehead et al., 2017). Thus, increased consumption rates may emerge more frequently in agricultural than in natural systems due to compensatory feeding.

However, our findings are in line with other studies from natural systems showing that although the consumers themselves are affected by warmer temperatures, the overall rate of resource consumption does not change significantly (Barton et al., 2009; O'Connor, 2009; Wen et al., 2023). This might be because all organisms involved are equally stressed by heat, or because herbivores' reduced activity levels (Terlau et al., 2023) balance out any increased metabolic demand. Another explanation is that, at certain temperature thresholds, resource consumption is no longer affected. For example, Lemoine et al. (2014) showed that overall leaf consumption rates increase with temperature between 20 and 30°C but do not increase further with increasing temperature. Therefore, although herbivory generally increases with temperatures, it does not under the extreme high temperatures of a heat wave event. Lastly, we believe that our results are more likely explained by the observed opposing heat wave effects on larval performance, as hosting fewer but larger and faster growing larvae under heat wave conditions may have evened out herbivory pressure on plants.

CONCLUSIONS

Here, we showed that the effects of heat waves on crop-pest dynamics are largely dependent on their timing and plant resistance. Although we found no heat wave impacts on plant herbivory and tuber yield, many changes occurred at the organismal level during the larval stage, which altered crop-pest dynamics, potentially impacting pest management practices. For instance, for insects that pupate in the soil, faster larval development may narrow the time window in which insecticides can be applied. Furthermore, more concentrated leaf damage in time may not be as important for tubers but may be important for crops where aboveground plant tissues are harvested. Under a future climate change scenario, we will need to consider the seasonality of these extreme weather events to effectively control pests. Finally, our results show that pest-resistant crop varieties, especially those with traits that impair post-heat wave insect recovery, may continue to be an important element for pest management under increasingly common heat waves.

AUTHOR CONTRIBUTIONS

William C. Wetzel and Zsofia Szendrei conceived the ideas; William C. Wetzel, Joshua S. Snook, and Luke N. Zehr designed the methods; Michael Kalwajtys and Luke N. Zehr collected the data; and Nalleli Carvajal Acosta analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

We are thankful to the Kellogg Biological Station staff, Josh Dykstra, Mark Hammond, Kevin Kahmark, Tim Kerney, and Brad Osborn. Paid and volunteer assistants included Olivia Jeris, Rachel Rantz, Jake Ruggiero, Sofia Maass, Cecilia Prada Cordero, Zane Ma, Georgia Seyfried, and Grant Miller. We thank Mark Otto and Chris Long for potato-specific advice and materials. This project was supported by Agriculture and Food Research Initiative Competitive grant number 2020-67013-31919 from the USDA National Institute of Food and Agriculture. This article is MSU Kellogg Biological Station contribution 2152.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Carvajal Acosta et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.k3j9kd5h4.

ORCID

Nalleli Carvajal Acosta https://orcid.org/0000-0002-7304-7139

William C. Wetzel https://orcid.org/0000-0001-5390-6824

REFERENCES

Alyokhin, A., M. Baker, D. Mota-Sanchez, G. Dively, and E. Graffus. 2008. "Colorado Potato Beetle Resistance to Insecticides." *American Journal of Potato Research* 85: 395–413.

Bader, C. A., and C. R. Williams. 2012. "Mating, Ovariole Number and Sperm Production of the Dengue Vector Mosquito *Aedes aegypti* (L.) in Australia: Broad Thermal Optima Provide the Capacity for Survival in a Changing Climate." *Physiological Entomology* 37: 136–144.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, et al. 2002. "Herbivory in Global Climate Change Research: Direct Effects of Rising Temperature on Insect Herbivores." *Global Change Biology* 8: 1–16.

Barton, B. T., A. P. Beckerman, and O. J. Schmitz. 2009. "Climate Warming Strengthens Indirect Interactions in an Old-Field Food Web." *Ecology* 90: 2346–51.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.

Bauerfeind, S. S., and K. Fischer. 2013. "Increased Temperature Reduces Herbivore Host-Plant Quality." *Global Change Biology* 11: 3272–82.

Bodlah, M. A., J. Iqbal, A. Ashiq, I. Bodlah, S. Jiang, M. A. Mudassir, M. T. Rasheed, and A. G. E. Fareen. 2023. "Insect Behavioral Restraint and Adaptation Strategies under Heat Stress: An Inclusive Review." *Journal of the Saudi Society of Agricultural Sciences* 22: 327–350.

Boiteau, G., A. Alyokhin, and D. N. Ferro. 2003. "The Colorado Potato Beetle in Movement." *The Canadian Entomologist* 135: 1–22.

Brás, T. A., J. Seixas, N. Carvalhais, and J. Jägermeyr. 2021. "Severity of Drought and Crop Losses Tripled over the Last Five Decades in Europe." *Environmental Research Letters* 16: 065012.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. Skaug, M. Maechler, and B. M. Bolker. 2017. "glmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *The R Journal* 9: 378–400.

Campitelli, B. E., A. J. Gorton, K. L. Ostevik, and J. R. Stinchcombe. 2013. "The Effect of Leaf Shape on the Thermoregulation and Frost Tolerance of an Annual Vine, *Ipomoea hederacea* (Convolvulaceae)." *American Journal of Botany* 100: 2175–82.

Carvajal Acosta, N., Z. Szendrei, L. Zher, W. Wetzel, J. Snook, and M. Kalwajtys. 2024. "Heat Wave Ontogenetic Timing Impacts on Potato Crop-Pest Dynamics [Dataset]." Dryad. https://doi.org/10.5061/dryad.k3j9kd5h4.

Chen, H., X. Zheng, M. Luo, J. Guo, G. S. Solangi, F. Wan, and Z. Zhou. 2018. "Effect of Short-Term High-Temperature Exposure on the Life History Parameters of *Ophraella communa*." *Scientific Reports* 8: 13969.

Cinto Mejía, E., and W. C. Wetzel. 2023. "The Ecological Consequences of the Timing of Extreme Climate Events." *Ecology and Evolution* 13: e9661.

Clissold, F. J., and S. J. Simpson. 2015. "Temperature, Food Quality and Life History Traits of Herbivorous Insects." *Current Opinion in Insect Science* 11: 63–70.

Cope, O. L., L. N. Zehr, A. A. Agrawal, and W. C. Wetzel. 2023. "The Timing of Heat Waves Has Multiyear Effects on Milkweed and Its Insect Community." *Ecology* 104: e3988.

da Silva, C. R., J. E. Beaman, J. P. Youngblood, V. Kellermann, and S. E. Diamond. 2023. "Vulnerability to Climate Change Increases with Trophic Level in Terrestrial Organisms." *Science of the Total Environment* 865: 161049.

Diamond, S. E., and J. G. Kingsolver. 2010. "Environmental Dependence of Thermal Reaction Norms: Host Plant Quality Can Reverse the Temperature-Size Rule." *The American Naturalist* 175: 1–10.

Domanda, C., V. Nuzzo, G. Montanaro, O. Falilla, and L. Rustioni. 2023. "Trichomes Affect Grapevine Leaf Optical Properties and Thermoregulation." *Theoretical and Experimental Plant Physiology* 35: 1–10.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. "Climate Extremes: Observations, Modeling, and Impacts." *Science* 289: 2068–74.

Ferro, D. N., J. A. Logan, R. H. Voss, and J. S. Elkinton. 1985. "Colorado Potato Beetle (Coleoptera: Chrysomelidae) Temperature-Dependent Growth and Feeding Rates." *Environmental Entomology* 14: 343–48.

Flanders, K. L., J. G. Hawkes, E. G. Radcliffe, and F. I. Lauer. 1992. "Insect Resistance in Potatoes: Sources, Evolutionary Relationships, Morphological and Chemical Defenses, and Ecogeographical Associations." *Euphytica* 61: 83–111.

Flores-Mejía, S., J. F. Guay, V. Fournier, and C. Cloutier. 2016. "The Influence of a Parasitoid's Response to Temperature on the Performance of a Tri-Trophic Food Web." *Ecological Entomology* 41: 431–441.

Forster, J., A. G. Hirst, and D. Atkinson. 2011. "How Do Organisms Change Size With Changing Temperature? The Importance of Reproductive Method and Ontogenetic Timing: Reproductive Method and Ontogenetic Timing." *Functional Ecology* 25: 1024–31.

Gilbert, J. P., J. M. Grady, and A. I. Dell. 2022. "Food Web Consequences of Thermal Asymmetries." *Functional Ecology* 36: 1887–99.

Hamann, E., C. Blevins, S. J. Franks, M. I. Jameel, and J. T. Anderson. 2021. "Climate Change Alters Plant–Herbivore Interactions." *New Phytologist* 229: 1894–1910.

Hare, J. D. 1990. "Ecology and Management of the Colorado Potato Beetle." *Annual Review of Entomology* 35: 81–100.

Harvey, J. A., R. Heinen, R. Gols, and M. P. Thakur. 2020. "Climate Change-Mediated Temperature Extremes and Insects: From Outbreaks to Breakdowns." *Global Change Biology* 26: 6685–6701.

Hlywka, J. J., G. R. Stephenson, M. K. Sears, and R. Y. Yada. 1994. "Effects of Insect Damage on Glycoalkaloid Content in Potatoes (*Solanum tuberosum*)." *Journal of Agricultural and Food Chemistry* 42: 2545–50.

Hodin, J., and L. M. Riddiford. 2000. "Different Mechanisms Underlie Phenotypic Plasticity and Interspecific Variation for a Reproductive Character in *Drosophilids* (Insecta: Diptera)." *Evolution* 54: 1638–53.

Iltis, C., P. Louâpre, F. Vogelweith, D. Thiéry, and J. Moreau. 2021. "How to Stand the Heat? Post-stress Nutrition and Developmental Stage Determine Insect Response to a Heat Wave." *Journal of Insect Physiology* 131: 104214.

Kingsolver, J. G., and L. B. Buckley. 2020. "Ontogenetic Variation in Thermal Sensitivity Shapes Insect Ecological Responses to Climate Change." *Current Opinion in Insect Science* 41: 17–24.

Kingsolver, J. G., and R. B. Huey. 2008. "Size, Temperature, and Fitness: Three Rules." *Evolutionary Ecology Research* 10: 251–268.

Klockmann, M., F. Günter, and K. Fischer. 2017. "Heat Resistance throughout Ontogeny: Body Size Constrains Thermal Tolerance." *Global Change Biology* 23: 686–696.

Kowalski, S. P., N. T. Eannetta, A. T. Hirzel, and J. C. Steffens. 1992. "Purification and Characterization of Polyphenol Oxidase From Glandular Trichomes of *Solanum berthaultii*." *Plant Physiology* 100: 677–684.

Lemoine, N. P., D. E. Burkepile, and J. D. Parker. 2014. "Variable Effects of Temperature on Insect Herbivory." *PeerJ* 2: e376.

Lenth, R. 2023. "emmeans: Estimated Marginal Means, aka Least-Squares Means. R Package Version 1.8.9." https://CRAN.R-project.org/package=emmeans.

Lesk, C., P. Rowhani, and N. Ramankutty. 2016. "Influence of Extreme Weather Disasters on Global Crop Production." *Nature* 529: 7584.

Lewis, W. J., J. C. van Lenteren, S. C. Phatak, and J. H. Tumlinson. 1997. "A Total System Approach to Sustainable Pest Management." *Proceedings of the National Academy of Sciences of the United States of America* 94: 12243–48.

Lowe, W. H., T. E. Martin, D. K. Skelly, and H. A. Woods. 2021. "Metamorphosis in an Era of Increasing Climate Variability." *Trends in Ecology & Evolution* 36: 360–375.

Mackey, A. P. 1977. "Growth and Development of Larval Chironomidae." *Oikos* 28: 270–75.

Maharijaya, A., and B. Vosman. 2015. "Managing the Colorado Potato Beetle; the Need for Resistance Breeding." *Euphytica* 204: 487–501.

Malakar, R., and W. M. Tingey. 2000. "Glandular Trichomes of *Solanum berthaultii* and Its Hybrids With Potato Deter Oviposition and Impair Growth of Potato Tuber Moth." *Entomologia Experimentalis et Applicata* 94: 249–257.

Maxwell, S. L., N. Butt, M. Maron, C. A. McAlpine, S. Chapman, A. Ullmann, D. B. Segan, and J. E. Watson. 2019. "Conservation Implications of Ecological Responses to Extreme Weather and Climate Events." *Diversity and Distributions* 25: 613–625.

Meehl, G. A., and C. Tebaldi. 2004. "More Intense, More Frequent, and Longer Lasting Heat Waves in the 21st Century." *Science* 305: 994–97.

Miller, S., K. Chua, J. Coggins, and H. Mohtadi. 2021. "Heat Waves, Climate Change, and Economic Output." *Journal of the European Economic Association* 19: 2658–94.

Neal, J. J., J. C. Steffens, and W. M. Tingey. 1989. "Glandular Trichomes of *Solatium berthaultii* and Resistance to the Colorado Potato Beetle." *Entomologia Experimentalis et Applicata* 51: 133–140.

Neven, L. G. 2000. "Physiological Responses of Insects to Heat." *Postharvest Biology and Technology* 21: 103–111.

Nielsen, M. E., and R. D. Papaj. 2015. "Effects of Developmental Change in Body Size on Ectotherm Body Temperature and Behavioral Thermoregulation: Caterpillars in a Heat-Stressed Environment." *Oecologia* 177: 171–79.

O'Connor, M. I. 2009. "Warming Strengthens an Herbivore-Plant Interaction." *Ecology* 90(2): 388–398.

Potter, K. A., G. Davidowitz, and H. A. Woods. 2011. "Cross-Stage Consequences of Egg Temperature in the Insect *Manduca sexta*." *Functional Ecology* 25: 548–556.

Prange, H. D. 1996. "Evaporative Cooling in Insects." *Journal of Insect Physiology* 42(5): 493–99.

Prange, H. D., and B. Pinshow. 1994. "Thermoregulation of an Unusual Grasshopper in a Desert Environment: The Importance of Food Source and Body Size." *Journal of Thermal Biology* 19: 75–78.

R Core Team. 2018. *R: A Language and Environment for Statistical Computing (4.2.1)*. Vienna: R Foundation for Statistical Computing.

Radcliffe, E. B. 1982. "Insect Pests of Potato." *Annual Reviews of Entomology* 27: 173–204.

Robinson, P. J. 2001. "On the Definition of a Heat Wave." *Journal of Applied Meteorology* 40: 762–775.

Sales, K., R. Vasudeva, and M. J. G. Gage. 2021. "Fertility and Mortality Impacts of Thermal Stress From Experimental Heatwaves on Different Life Stages and Their Recovery in a Model Insect." *Royal Society Open Science* 8: 201717.

Schrevens, S. J., E. Frago, A. Stens, P. W. De Jong, and J. J. Van Loon. 2017. "Contrasting Effects of Heat Pulses on Different Trophic Levels, an Experiment With a Herbivore-Parasitoid Model System." *PLoS One* 12: e0176704.

Shinner, R., J. S. Terblanche, and S. Clusella-Trullas. 2020. "Across-Stage Consequences of Thermal Stress Have Trait-Specific Effects and Limited Fitness Costs in the Harlequin Ladybird, *Harmonia axyridis*." *Evolutionary Ecology* 34: 555–572.

Stamp, N. E., and M. D. Bowers. 1990. "Variation in Food Quality and Temperature Constrain Foraging of Gregarious Caterpillars." *Ecology* 71: 1031–39.

Steven, D. J. 2004. "Pupal Development Temperature Alters Adult Phenotype in the Speckled Wood Butterfly, *Pararge aegeria*." *Journal of Thermal Biology* 29: 205–210.

Terlau, J. F., U. Brose, N. Eisenhauer, A. Amyntas, T. Boy, A. Dyer, A. Gebler, et al. 2023. "Microhabitat Conditions Remedy Heat Stress Effects on Insect Activity." *Global Change Biology* 29: 3747–58.

Tingey, W. M., and S. L. Sinden. 1982. "Glandular Pubescence, Glycoalkaloid Composition, and Resistance to the Green Peach Aphid, Potato Leafhopper, and Potato Flea Beetle in *Solanum berthaultii*." *American Potato Journal* 59: 95–106.

USDA Agricultural Marketing Service. 2011. "United States Standards for Grades of Potatoes." https://www.ams.usda.gov/sites/default/files/media/Potato_Standard%5B1%5D.pdf.

Van Dievel, M., R. Stoks, and L. Janssens. 2017. "Beneficial Effects of a Heat Wave: Higher Growth and Immune Components Driven by a Higher Food Intake." *Journal of Experimental Biology* 220: 3908–15.

Vasudeva, R. 2023. "Experimental Evidence for Stronger Impacts of Larval but Not Adult Rearing Temperature on Female Fertility and Lifespan in a Seed Beetle." *Evolutionary Ecology* 37: 545–567.

Veteli, T. O., K. Kuokkanen, R. Julkunen-Tiitto, H. Roininen, and J. Tahvanainen. 2002. "Effects of Elevated CO_2 and Temperature on Plant Growth and Herbivore Defensive Chemistry." *Global Change Biology* 8: 1240–52.

Voigt, W., J. Perner, A. J. Davis, T. Eggers, J. Schumacher, R. Bährmann, B. Fabian, et al. 2003. "Trophic Levels Are Differentially Sensitive to Climate." *Ecology* 84: 2444–53.

Wen, D., Y. Guan, L. Jiang, S. Chen, F. Chen, B. Liu, Ü. Niinemets, and Y. Jiang. 2023. "Heat-Stress Induced Sesquiterpenes of *Chrysanthemum nankingense* Attract Herbivores but Repel Herbivore Feeding." *Arthropod-Plant Interactions* 17: 111–122.

Wetzel, W., P. Hahn, B. Inouye, N. Underwood, S. V. T. Whitehead, K. Abbott, E. Bruna, et al. 2023. "Plant Size, Latitude, and Phylogeny Explain Within-Population Variability in Herbivory." *Science* 382: 679–683.

Whitehead, S. R., M. M. Turcotte, and K. Poveda. 2017. "Domestication Impacts on Plant-Herbivore Interactions: A Meta-analysis." *Philosophical Transactions of the Royal Society B: Biological Sciences* 372: 20160034.

Williams, C. M., L. B. Buckley, K. S. Sheldon, M. Vickers, H.-O. Pörtner, W. W. Dowd, A. R. Gunderson, K. E. Marshall, and

J. H. Stillman. 2016. “Biological Impacts of Thermal Extremes: Mechanisms and Costs of Functional Responses Matter.” *Integrative and Comparative Biology* 56: 73–84.

Xing, K., A. A. Hoffmann, and C.-S. Ma. 2014. “Does Thermal Variability Experienced at the Egg Stage Influence Life History Traits across Life Cycle Stages in a Small Invertebrate?” *PLoS One* 9: e99500.

Yang, Y., N. E. Stamp, and T. L. Osier. 1996. “Effects of Temperature, Multiple Allelochemicals and Larval Age on the Performance of a Specialist Caterpillar.” *Entomologia Experimentalis et Applicata* 79: 335–344.

Zhang, W., V. H. W. Rudolf, and C.-S. Ma. 2015. “Stage-Specific Heat Effects: Timing and Duration of Heat Waves Alter Demographic Rates of a Global Insect Pest.” *Oecologia* 179: 947–957.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Acosta, Nalleli Carvajal, Luke N. Zehr, Joshua S. Snook, Zsofia Szendrei, Michael Kalwajtys, and William C. Wetzel. 2024. “Heat Wave Impacts on Crop-Pest Dynamics are Dependent upon Insect Ontogeny and Plant Resistance.” *Ecosphere* 15(10): e70028. https://doi.org/10.1002/ecs2.70028