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Source: Environmental Entomology, 51(1) : 216-221

Published By: Entomological Society of America

URL: <https://doi.org/10.1093/ee/nvab136>

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Plant-Insect Interactions

Into the Wild: Evidence for the Enemy Release Hypothesis in the Invasive Callery Pear (*Pyrus calleryana*) (Rosales: Rosaceae)

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Subject Editor: Christopher M. Ranger

Received 19 September 2021; Editorial decision 1 November 2021

Abstract

Wild Callery pear (*Pyrus calleryana* Decne.) results from a cross between various cultivars of *P. calleryana* and any other *Pyrus* individual. While many cultivars of this species are still commercially produced and sold for horticultural purposes in the United States, Callery pear is a detrimental invasive species that encroaches on many managed and natural areas, damages equipment and injures people, pets, and livestock with its thorny branches, and likely causes detrimental ecological impacts. Despite its importance as an invasive species, the mechanisms behind Callery pear's invasion and spread are unclear. To identify potential drivers of invasion, we quantified feeding of generalist and specialist herbivores on Callery pear and four native tree species, based on insect host ranges, with choice and no-choice experiments followed by field surveys of herbivory on these same tree species. Feeding by all herbivores was lower on Callery pear than on native tree species in no-choice assays. Specifically, feeding on Callery pear was moderate by generalists and very low by specialists. Specialist feeding on Callery pear was comparable to native species in choice assays but was significantly reduced in no-choice assays. Reduced specialist feeding along with moderate generalist feeding on Callery pear in the field provides evidence for the Enemy Release Hypothesis as a potential driving mechanism behind its invasion success.

Key words: herbivore, enemy release hypothesis, *Hyphantria cunea*, invasive species, *Malacasoma americanum*

The economic and environmental impacts of invasive species are an important and omnipresent topic in today's global economy and environment. Global economic trading has led to an exponential increase in the number of non-native species being introduced into novel ecosystems, both intentionally and accidentally (Westphal et al. 2007, Aukema et al. 2010, Dawson et al. 2017, Seebens et al. 2017). While most highly impactful invasive invertebrates and vertebrates are accidentally introduced, nearly all invasive woody plants are purposely brought to new countries, and varieties or cultivars can often be easily purchased and escape cultivation or containment. Chinese privet (*Ligustrum sinense* Lour. [Lamiales: Olaceae]), for example, has been widely planted throughout managed landscapes in the southeastern U.S., and its escape into natural areas has resulted in detrimental impacts on pollinators (Hanula and Horn 2011a, b) and native plant communities (Hudson et al. 2013) and has altered nitrogen and carbon dynamics (Mitchell et al. 2017). Further, every known invasive tree and shrub in the United States was intentionally

introduced via the horticulture trade (Reichard and White 2001, Lalk et al. 2021) and many can still be purchased (Beaury et al. 2021).

At least 50,000 invasive species are estimated to be in the U.S. and, with ever-increasing global trade, understanding invasive species spread and using this information to guide management strategies is of the utmost importance (Pimentel et al. 2005, Lodge et al. 2016). Spread dynamics and impacts of many common invasive plants are well-understood [e.g. cogongrass (*Imperata cylindrica* (L.) P. Beauv.) (Poales: Poaceae) (Estrada and Flory 2015), cheatgrass (*Bromus tectorum* L. [Poales: Poaceae]) (Morrow and Stahlman 1984), water hyacinth (*Eichhornia crassipes* Mart. [Commelinales: Pontederiaceae]) (Dersseh et al. 2019)] while others, like Callery pear (*Pyrus calleryana* Decne.) (despite their large geographic range and high abundance) remain somewhat of a mystery. Considering the recent North American invasion of the spotted lanternfly (*Lycorma delicatula* White, 1845 [Hemiptera: Fulgoridae]) and its close

association with another common but understudied invasive species tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle [Sapindales Simaroubaceae]) (Barringer et al. 2015, Dara et al. 2015), it is imperative that we understand the ecology of these invasive woody plants in our native ecosystems (Lalk et al. 2021).

Release from population suppression due to reduced feeding by specialist herbivores (this being termed the Enemy Release Hypothesis (ERH) (Keane and Crawley 2002)) is one important factor that can help facilitate the spread of invasive species. The ERH is one of the most cited hypotheses in invasion ecology, and meta-analyses (e.g. Liu and Stiling 2006, Meijer et al. 2016) have generally found that richness of insect herbivore communities is greater on native plants versus introduced plants due to herbivores preferring native species over introduced species. This difference is disproportionately caused by a reduction in specialist feeders on introduced plants; herbivory on native plants also tends to be greater than on introduced plants.

This release on introduced plants may then be compounded by increased feeding by both specialists and generalists on surrounding native species (Maron and Vila 2001). Other hypotheses that may explain the recent invasion of *P. calleryana* include the Evolution of Competitive Ability (EICA) hypothesis and the Novel Weapons (NW) hypothesis. The EICA states that resources no longer used in defense may be put towards growth or reproduction, allowing invasive species to rapidly evolve in novel regions to outcompete native species (Blossey and Notzold 1995). The NW hypothesis states that some invasive organisms transform the environment through novel biochemical weapons (i.e., allelopathy) which then serve to reduce growth and development of surrounding species (Callaway and Ridenour 2004).

P. calleryana is native to East and Southeast Asia and was introduced into the U.S. in the early 20th Century (Culley 2017). *P. calleryana* cultivars are some of the most widely planted ornamental trees in the eastern U.S., the most common of which is the Bradford pear (*P. calleryana* var. 'Bradford'). Within its native range, it can occupy a variety of habitats, including plains, forests, thickets, and slopes (Culley and Hardiman 2007). It is frequently planted in managed landscapes as an ornamental tree and this, along with its wide range of habitat tolerance, disease resistance, and resistance to herbivory, has contributed to this tree's successful invasion of natural and managed areas across the eastern U.S. (Culley and Hardiman 2007, EDDMapS 2021) and its presence on global invasive species lists (Global Invasive Species Database 2008). Despite this invasive plant's increasing abundance in natural areas, we know very little about herbivory in its native range or the mechanisms behind its successful spread; filling this knowledge gap will help guide future management efforts as well as regulatory measures.

Our objective was to examine the potential for the ERH as a driving mechanism behind Callery pear's invasion in the eastern U.S. by quantifying herbivory of generalist and specialist arthropods in laboratory feeding assays and field surveys. Specifically, we hypothesized that Callery pear invasion would be supported by the release of natural enemies through reduced herbivory by specialists and low to moderate feeding by generalists.

Methods

Herbivore Collection

We used generalist/specialist and native/non-native herbivores in our feeding assays, specifically, fall webworm (*Hyphantria cunea* Drury, 1773; FWW, native generalist herbivore), eastern tent caterpillar (*Malacosoma americanum* F., 1793; ETC, native specialist herbivore on Rosaceae), and Japanese beetle (*Popillia japonica* Newman, 1841;

JB, non-native generalist herbivore). On 13 June 2019, 11 FWW egg masses and associated egg-laying females were collected from persimmon (*Diospyros virginiana* L. [Ericales: Ebenaceae]) trees adjacent to Clemson University (34.700136, -82.796767) and left outside in a mesh-covered cage to protect from predators and parasitoids. After eclosion, ca. one week after collection, neonates were transferred into Bug Dorm 4M-4590 mesh cages (MegaView Science Co., Ltd., Taiwan) in the Clemson Forest Health Lab and were fed persimmon leaves *ad libitum* with a 16:8 h L:D cycle to mimic natural conditions. On 24 March 2020, three tents containing ETC larvae were removed from a single black cherry (*Prunus serotina* [Rosales: Rosaceae]) tree in the town of Central, SC (34.703068, -82.790549), transferred to Bug Dorms and fed black cherry leaves *ad libitum*. Between 7 and 13 June 2020, 420 adult JB were collected from a variety of woody landscape plants in Watkinsville, GA (33.8806053, -83.4928045) and transferred to Bug Dorms in Clemson, SC and fed *Rosa* leaves *ad libitum*. All herbivores were starved for 48 h prior to feeding assays.

Experimental Design

We assessed herbivore feeding preferences using a randomized complete block design with choice and no-choice treatments. Choice tests consisted of one 6.45 cm² disc per leaf per host species, and no-choice tests consisted of five leaf discs from the same species (Fig. 1). Tree species were chosen based on the recorded host range and phenology of each herbivore species; each feeding assay consisted of Callery pear, one preferred host, two less preferred hosts, and one nonhost to act as a negative control (Table 1). For FWW and ETC, feeding trials consisted of five leaf discs organized in a circle around the edge of a 150 x 15 mm Petri dish, and five caterpillars per dish. For JB, whole leaves were fed to five beetles per Bug Dorm and initial leaf area was measured using ImageJ (Schneider et al. 2012). Densities of individuals were maintained for the duration of the feeding trials. Dead individuals were replaced with live individuals when necessary.

Caterpillars were randomly selected from Bug Dorms and placed in Petri dishes at second and/or third instar and starved for 48 h to ensure feeding. Japanese beetles were kept in ventilated glass jars during the starvation period. Choice and no-choice assays were performed concurrently with trials being added as additional caterpillars reached second or third instar or as additional beetles were collected. Herbivores were allowed to feed for 120 h (FWW), 72 h (JB), or 24 h (ETC) before herbivory quantification. Due to leaf drying and curling, a digital program to measure leaf area consumed could not be used. Instead, the proportion of discs/leaves consumed was visually quantified by splitting each disc and leaf into eight, equally sized quadrats and visually estimating the proportion of each quadrat that was consumed. Proportions were then summed across each disc or leaf to obtain a total proportion of disc/leaf consumed. Proportion consumed was then multiplied by the total disc

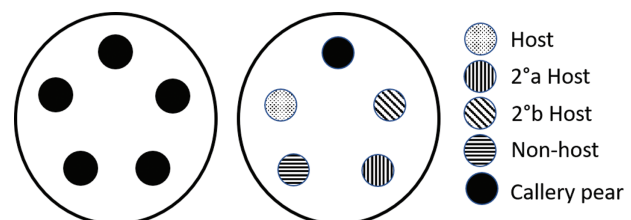


Fig. 1. Experimental design of choice (right) and no-choice (left) assays. Leaf discs were randomly placed in cages.

Table 1. Summary of hosts, besides *P. calleryana*, used in choice and no-choice feeding assays per herbivore

	1° Host	2°a Host	2°b Host	Nonhost
FWW	Persimmon (<i>Diospyros virginiana</i> L.)	Mockernut hickory (<i>Carya alba</i> L.)	Sweetgum (<i>Liquidambar styraciflua</i> L.)	Tulip poplar (<i>Liriodendron tulipifera</i> L.)
ETC	Black cherry (<i>Prunus serotina</i> Ehrh.)	Hawthorn (<i>Crataegus Tourn. ex L.</i>)	<i>Rosa</i> L.	Tulip poplar
JB	Black raspberry (<i>Rubus occidentalis</i> L. 1753)	Mockernut hickory	Red maple (<i>Acer rubrum</i> L. 1753)	Tulip poplar

FWW, fall webworm; ETC, eastern tent caterpillar; JB, Japanese beetle.

or leaf area to obtain a leaf area consumed. Leaf area consumption is a well-accepted method for measuring herbivory in feeding assays (e.g. Eberl et al. 2020). While visual estimation has been shown to be an accurate and precise method of quantifying herbivory (Johnson et al. 2016), one individual measured all leaf discs and whole leaves to reduce variation and biases.

Herbivory Surveys

On 3 September 2021, we surveyed Callery pear and three of the native tree species used in feeding trials (red maple, black cherry, mockernut hickory) for herbivory. We sampled small trees (2–4" DBH) in the Clemson Experimental Forest (34.744243, –82.838293) by removing a single branch from the lower, middle, and upper crown, and examining 10 randomly selected individual leaves, across different phenological ages, from each branch for herbivore damage (i.e., chewing, leaf miners, piercing-sucking insect damage). On those leaves with herbivore damage, proportion of the leaf eaten was estimated in the same manner as above.

Statistical Analyses

A total of 28 FWW, 30 ETC, and 14 JB feeding trial replications were completed. Choice and no-choice tests were analyzed separately, and all analyses were performed for all three herbivores in the same manner. No data met assumptions for parametric analyses, thus nonparametric analyses were used. To quantify the feeding responses of herbivores to Callery pear foliage, we performed a Kruskal-Wallis Test with leaf area consumed (cm²) as the response variable and tree species as the independent variable. Significant Kruskal-Wallis results were followed with a nonparametric posthoc analysis using a Dunn Test in the R package 'FSA' (Ogle et al. 2017). A Wilcoxon signed-rank test was used to compare feeding of each herbivore between choice and no-choice tests. Herbivory surveys were analyzed in the same manner, except proportion of leaf area consumed as the dependent variable. A generalized linear model (GLM) was then performed to identify feeding estimates on each tree species for both choice and no-choice assays. All statistical analyses were completed using R (R Core Team 2020).

Results

Choice Tests

Feeding preferences of all three herbivore species differed significantly among and between the tree species tested (Table 2). FWW fed least on Callery pear and most on its secondary host, black cherry, followed by its primary host, persimmon, another secondary host, sweetgum, and then its nonhost tulip poplar ($X^2_4 = 36$, $P < 0.001$). ETC fed most on its primary host, black cherry, followed by its secondary host, *Rosa*, another secondary host, hawthorn, then Callery pear, and finally the nonhost, tulip poplar ($X^2_4 = 113.72$, $P < 0.001$).

JB fed most on its primary host, *Rubus*, followed by the two secondary hosts mockernut hickory and red maple, and least on the nonhost tulip poplar and Callery pear ($X^2_4 = 12.44$, $P = 0.014$).

No-Choice Tests

Feeding preferences of all herbivores differed significantly among and between tree species (Table 2). FWW fed the least on Callery pear and the most on sweetgum followed by persimmon, and comparably on black cherry and mockernut hickory ($X^2_4 = 29.827$, $P < 0.001$). ETC feeding patterns were the same for no-choice as for choice experiments ($X^2_4 = 413.88$, $P < 0.001$). JB fed most on *Rubus* followed by tulip poplar, mockernut hickory, red maple, and least on Callery pear ($X^2_4 = 24.101$, $P < 0.001$).

All three herbivores' feeding preferences changed significantly in no-choice assays compared with choice assays. Overall, leaf consumption by all three herbivore species declined in no-choice assays. FWW significantly increased leaf area consumption across all species except persimmon ($W = 13,889$, $P < 0.001$). ETC significantly reduced feeding of all species in no-choice assays and this reduction was most significant with Callery pear ($W = 8,041.5$, $P < 0.0001$). JB feeding significantly increased on *Rubus* and mockernut hickory in no-choice assays but not the other three species tests ($W = 1,696$, $P = 0.004$).

Herbivory Surveys

Herbivory estimates differed significantly among tree species ($X^2_{16} = 90.1217$, $P < 0.0001$) (Fig. 2). Herbivory (mean proportion of leaf consumed \pm SE) was lowest on CP (0.0034 ± 0.0019) and highest on black cherry (0.0851 ± 0.0265). Mockernut hickory had the second-highest herbivory (0.0597 ± 0.0241), and red maple had the second-lowest herbivory (0.0282 ± 0.0097). There were no significant differences among branches (i.e., top, middle, lower) with regards to herbivory estimates ($X^2_{16} = 12.5274$, $P = 0.7069$).

Discussion

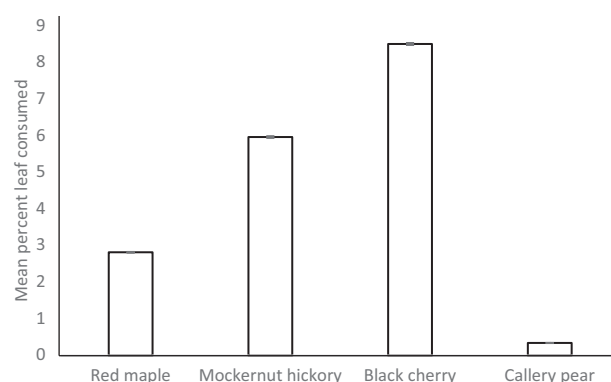
Many invasive plants in North America originate from horticultural selections or were purposely brought to this continent for planting in managed landscapes (Beaury et al. 2021) and it is important that both practitioners and landowners are aware of potential detriments that may result from widespread planting of these species and cultivars. For example, common lantana (*Lantana camara* L.), a popular landscape plant that is often planted to attract butterflies, can become invasive in natural areas and negatively impact several ecological attributes (Sharma et al. 2005). Examples like this underscore the importance of knowing how landscape plants may impact natural areas because, as history has shown, many popular landscape plants can and do escape into natural ecosystems.

Callery pear's ability to grow, spread, and reproduce in a wide range of environments suggests biotic interactions, rather than

Table 2. Summary of choice and no-choice feeding experiments for fall webworm (FWW), eastern tent caterpillar (ETC), and Japanese beetle (JB)

Study	Callery pear	Persim-mon	Black cherry	Hickory	Tulip poplar	Sweet gum	Red maple	Hawthorn	Rosa	Black raspberry
FWW feeding (avg cm ² ± SE)	Choice 0.123 ± 0.014e	2.416 ± 0.072b	5.042 ± 0.004a	0.163 ± 0.014c	-	0.765 ± 0.059d	-	-	-	-
	No-choice 0.786 ± 0.009d	1.193 ± 0.012b	0.869 ± 0.009c	0.784 ± 0.010a	-	1.612 ± 0.013d	-	-	-	-
ETC feeding (avg cm ² ± SE)	Choice 3.13 ± 0.060d	-	5.034 ± 0.004a	-	0 ± 0e	-	-	3.716 ± 0.046c	4.788 ± 0.030b	-
	No-choice 1.473 ± 0.012d	-	3.993 ± 0.011b	-	0.002 ± <0.001e	-	-	3.589 ± 0.013c	4.329 ± 0.010a	-
JB feeding (avg cm ² ± SE)	Choice 0.771 ± 0.117d	-	-	6.154 ± 0.485ab	1.656 ± 0.153c	-	4.757 ± 0.700b	-	-	8.785 ± 1.012a
	No-choice 0.255 ± 0.006b	-	-	0.494 ± 0.012a	0.715 ± 0.015b	-	0.508 ± 0.013a	-	-	1.067 ± 0.025a

Different letters within feeding studies denote significant differences across tree species using a Dunn test with a Holm *P*-value adjustment.

**Fig. 2.** Mean percent of each leaf eaten (± SE) during field surveys in the Clemson Experimental Forest on red maple, mockernut hickory, black cherry, and Callery pear.

abiotic factors (e.g., precipitation, temperature), as the limiting factor for pest status in its native range. We examined the ERH as a potential mechanism facilitating Callery pear invasion through feeding assays and herbivory surveys. How generalist and specialist herbivores respond to no-choice feeding assays can help predict what might happen in monoculture field scenarios which are common with invasive plants such as Callery pear. Generalist herbivore species require a wide breadth of host species to avoid accumulating too much of any one secondary metabolite (Bernays and Graham 1988). Generalists may also be avoiding predators or balancing nutrients by altering their feeding preferences (Lefcheck et al. 2013). In cases where generalist herbivores do not have a wide variety of food choices, they tend to reduce their feeding of any one species, especially if those species contain novel, or particularly toxic, secondary metabolites (Jogesh et al. 2008). Specialists, as the name suggests, require a narrower host range and have adapted to process certain secondary metabolites (Williams and Sahli 2016). In the case of invasive species, reduced feeding by specialists provides evidence for the ERH which assumes that specialist natural enemies provide the most population suppression in the plant's native range (Van Driesche and Reardon 2017).

Generalists in both cases responded as we expected with reduced overall feeding in no-choice assays; however, specific responses were dependent on their invasive status. The native generalist herbivore, FWW, increased consumption on Callery pear while the invasive generalist, JB, consumed slightly less than FWW. And, although FWW increased its consumption of Callery pear in no-choice assays compared with choice assays, total leaf consumption in no-choice assays declined overall for all species. Increased feeding by native generalists may facilitate the spread of invasive woody plants by inducing additional plant growth while not reducing plant reproductive capacity (Vila et al. 2005) and this has already been shown in Callery pear with generalist herbivore grasshoppers (Gawkins 2019).

While ETC is considered a specialist on Rosaceous species (which includes *Pyrus*) their Callery pear consumption was reduced in no-choice tests, possibly suggesting the presence of novel or toxic secondary metabolites. Previous studies have linked reduced specialist herbivory to increased invasive plant spread (Joshi and Vrieling 2005). Low to moderate feeding by generalists and low feeding by specialists provides evidence for the ERH in the Callery pear system in that specialist herbivores are not, and apparently will not, consume enough Callery pear to provide population regulation or prevent continued spread of this invasive plant. Low rates

of herbivory on Callery pear compared to native trees also provides evidence that herbivores are not providing population control or preventing spread of the invasive. However, it is important to note that two factors, arrangement of leaves and number of choices provided, were not analyzed in this experiment and may have an effect on herbivore feeding (Raffa et al. 2002).

Increased feeding in no-choice experiments compared to choice experiments by the non-native generalist JB also suggests that Callery pear invasion may create a positive feedback loop leading to an “invasional meltdown” (Simberloff and Von Holle 1999, Gandhi and Herms 2010, Heimpel et al. 2010, Kuebbing 2020). Other invasive woody plants, such as Chinese privet, amur honeysuckle, and European buckthorn, have been recorded as causing invasional meltdown, directly and indirectly, impacting pollinators, herbivores, and native plants (Heneghan et al. 2006, Heimpel et al. 2010, Hanula and Horn 2011a, b, Hoven et al. 2017). In the case of Callery pear, several mechanisms may play a role in a future invasional meltdown. Should reduced herbivory on Callery pear indicate a preference of herbivores to native species, this would cause additional stress on natives and further release Callery pear to grow and reproduce. Additional studies investigating herbivore responses in field settings along a gradient of *P. calleryana* invasion are warranted to examine how herbivores alter their feeding on native trees in the presence or absence of *P. calleryana* to fully test this hypothesis.

It is also possible that the species composition and diversity of surrounding vegetation affected the establishment and spread of Callery pear into new habitats (“Biotic Resistance Hypothesis” and “Biotic Indirect Effects Hypothesis”) (Maron and Vila 2001). Should these mechanisms play a role in the invasion of Callery pear, phylogenetic distance between Callery pear and species present would affect which, and how, arthropods were most affected, and therefore, the success of Callery pear would be dependent on site conditions and community composition.

This study also has implications for future studies in the *P. calleryana* system with regards to the EICA and NW hypotheses. With release from herbivores, *P. calleryana* may be able to allocate resources to areas of growth to outcompete native species. However, Merritt et al. (2014) found that photosynthetic ability of *P. calleryana* was comparable to native species, suggesting that other factors are likely at play. Work is currently underway to test the presence of allelopathic chemicals in *P. calleryana* tissue (J. Hartshorn, unpublished data).

Callery pear is a successful plant invader in the U.S., and our knowledge of what facilitates this invasion success is still in its infancy. To further elucidate driving mechanisms behind Callery pear and potential future interactions with native flora and fauna, additional experiments are warranted to quantify functional and numerical responses of arthropod herbivores to Callery pear foliage. Examining leaf nutrition and root allelopathy is also necessary to answer questions related to potential drivers behind Callery pear invasion such as the EICA (Callaway and Ridenour 2004) and NW hypotheses (Bais et al. 2003). It is likely that successful invaders like Callery pear benefit from several driving mechanisms.

Our results show that specialist and generalist herbivores respond to Callery pear in ways that promote Callery pear growth and reproduction. A side effect of this may be further suppression of native plants through a push-pull system where herbivores are driven away from *P. calleryana* and towards native species. Our results also provide evidence for the ERH and point towards additional driving mechanisms behind Callery pear invasion. As Callery pear continues to encroach into natural and managed lands, this spread is likely to impact both native and invasive arthropod herbivores, as well as additional arthropod and vertebrate guilds (Narango et al. 2018).

These interactions likely impact multiple trophic levels, potentially resulting in an invasional meltdown. Callery pear is a serious threat and research is necessary to understand the drivers behind its continued spread.

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