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Leaf phenology and freeze tolerance of the invasive tree Pyrus calleryana (Roseaceae) and potential native competitors

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Leaf phenology and freeze tolerance of the invasive tree *Pyrus calleryana* (Roseaceae) and potential native competitors[1]

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Abstract. *Pyrus calleryana* is one of the most problematic invasive species in the eastern United States. The mechanisms that enable *Py. calleryana* to establish and outcompete native plants are not fully understood but likely include a profile of advantageous traits. Extended leaf phenology is a characteristic noted in many woody invasive plants. Leaf phenology of *Py. calleryana* and two native woody species, *Populus deltoides* and *Platanus occidentalis*, was observed in natural areas near Dayton, OH from December 2019 to November 2020. A frost event in May also gave us the serendipitous opportunity to assess frost tolerance of these species. We found that *Py. calleryana* began leafing out almost a month before its native competitors in the spring and kept its leaves on significantly longer than both *Po. deltoides* and *Pl. occidentalis* throughout the fall. After the frost event, almost every leaf on *Pl. occidentalis* died and almost 70% of the leaves on *Po. deltoides* were damaged; however, *Py. calleryana* exhibited damage on only 6% of its leaves. Our study suggests that *Py. calleryana* has a nearly 1-mo advantage in leaf phenology in both spring and fall, and much greater frost tolerance, as compared with native species. These attributes likely contribute to its capacity to outcompete native trees in early successional habitats.

Key words: Callery pear, exotic species, invasive species, *Platanus occidentalis*, *Populus deltoides*

Invasive plants are a significant threat to biodiversity and ecosystem function in a variety of habitats and understanding the mechanisms that enable invasive species to gain dominance is a pressing scientific and conservation concern (USOTA 1993, Pimentel *et al*. 2000, Sakai *et al*. 2001, Wolfe 2002, Van Kleunen *et al*. 2010, Gorchov *et al*. 2021). Woody plant invasion into grasslands is a specific and particularly challenging situation in many ecosystems in eastern North America (Webster *et al*. 2006). Preventing woody encroachment is necessary for maintaining the structure and function of grasslands (Webster *et al*. 2006), and old-field succession from grassland to forest can be disrupted by invasive species (Cramer *et al*. 2008). Postagricultural fields and other fallow grasslands are characterized by high light availability that is conducive to ecological invasion by some species, and successful invasion of these habitats may drive the system toward novel species combinations and woody plant dominance, thwarting conservation goals (Cramer *et al*. 2008, Flory and Clay 2010).

Pyrus calleryana (Callery pear) is an important invasive tree in the eastern United States that is particularly problematic in grassland habitats. Originating in temperate East Asia, *P. calleryana* was introduced to the USA and developed as a landscape ornamental plant (Culley and Hardiman 2007, Sapkota *et al*. 2021). This species escaped cultivation and has become a significant threat to grassland systems (Vincent 2005, Culley *et al*. 2011). Recent work has focused on developing a clearer understanding of the biology of *P. calleryana* invasion (Hartshorn *et al*. 2022) and techniques to control this species in habitats of conservation concern (Coyle *et al*. 2021). *Pyrus calleryana* is bird dispersed (Culley 2017) and has an aggressive and ecologically important sprouting response to disturbance (Woods *et al*. 2021), creating the potential for widespread establishment and persistence; however, the mechanisms this species uses to establish dominance are not fully understood.

An extended leaf phenology is an important mechanism that creates competitive advantages for some invasive species. The timing of blooming, flowering, and seed dispersal has been shown to

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have consequences for pollination, light competition, predation, and species survivorship in some systems (Ghazoul 2004, Miller-Rushing *et al*. 2010, McEwan *et al*. 2011). Invasive species often have earlier leafing-out periods and longer leaf duration during the growing season than native species, leading to increased potential for solar energy acquisition and competitive advantage. For example, the invasive shrub *Lonicera maackii* had an earlier leaf out and later leaf drop when compared with common native shrubs (McEwan *et al*. 2009). A pattern of extended leaf phenology was also detected in *Berberis thunbergii*, a shrub that invades deciduous forests in the northeastern USA (Xu *et al*. 2007). When compared with two native understory shrubs, *B. thunbergii* leaf expansion initiated earlier than native shrubs (Xu *et al*. 2007). Indeed, Fridley (2012) found that most nonnative woody invasive species capitalized on an extended autumn phenology, a behavior that was absent in native species across multiple phylogenetic groups. An extended phenology may create a competitive advantage through providing additional opportunity for carbon gain during ecological invasion (Fridley 2012).

We observed the leaf phenology of *Py. calleryana* and two native tree species (*Populus deltoides* and *Platanus occidentalis*) in three grassland sites in the vicinity of Dayton, OH. In regional grassland habitats, both *Pl. occidentalis* and *Po. deltoides* regularly co-occur with *Py. calleryana* and, although the size at maturity is much larger for both native species, competition in open habitats during the sapling stage may be relevant for longer-term competitive outcomes. The overall objective of this study was to quantify the leaf phenology of *P. calleryana* as compared with native early successional woody species that do not exhibit similar invasive behavior in regional grasslands. We hypothesized that (H_1) *Py. calleryana* would leaf out significantly before native woody species and (H_2) have an extended phenology in the fall. A late spring freeze (see details below) provided a serendipitous opportunity to examine differences in freeze tolerance for these species and we hypothesized that (H_3) *Py. calleryana* would be more resistant to freezing temperatures.

Methods. STUDY DESIGN. Observations for this study took place within the Medlar Conservation Area (39°36′09.4″N, 84°16′25.2″W) and Stillwater Conservation Area (39°50′24.8″N, 84°14′17.9″W) near Dayton, OH. Sites were selected on the basis of the presence of the three study species, with individual stems < 3 m tall, that were growing in proximity in similar environmental conditions. These sites are managed by the Five Rivers Metroparks of Dayton, OH and are within a 50-km radius of one another. All three sites were previously agricultural fields and have been managed as grasslands for conservation purposes by the Five Rivers Metroparks. In the Medlar Conservation Area, 10 *Py. calleryana*, 10 *Pl. occidentalis*, and 9 *Po. deltoides* trees were monitored. At the Stillwater Conservation Area, five *Py. calleryana* and five *Pl. occidentalis* were selected for observation; however, only two *Pl. deltoides* were identified in proximity with the other species and on October 2, 2020 these two trees were accidentally cut down during maintenance activities. For the purposes of statistical analysis each date has $n = 15$ observations for *Py. calleryana*, $n = 15$ observations for *Pl. occidentalis*, and $n = 11$ trees before October 2, 2020 and $n = 9$ *Pl. deltoides* observations after the accidental removal.

From November 2019 to November 2020 we monitored the vegetative phenology of the trees as they progressed throughout the year. To do so, a single branch was selected and tagged on each tree. During each observation, starting at the outermost bud and moving inward, the first 10 buds of the branch were counted, and the phenotypic vegetative features of each leaf were recorded. If multiple leaves grew out of the same bud, we selected the leaf closest to the stem. In the winter of 2019–20, the leaves were checked once a month. Beginning in February 2020, we monitored leaves every 3 days to document leaf development until all trees had leaves that were fully developed and had reached summer green color. During the summer, trees were observed once a month until autumnal color change began, at which point leaves were observed once a week until they abscised. Observations were based on the following leaf development categories: 1, bud dormant; 2, leaf blade visible; 3, entire leaf exposed; 4, entire leaf exposed and flat; 5, summer green; 6, leaf different from summer color; 7, leaf at fall color; 8, leaf abscission.

STATISTICAL ANALYSIS. All analyses were done using R v. 4.1.3 (R Core Team 2022) and data visualizations were created in ggplot2 (Wickham

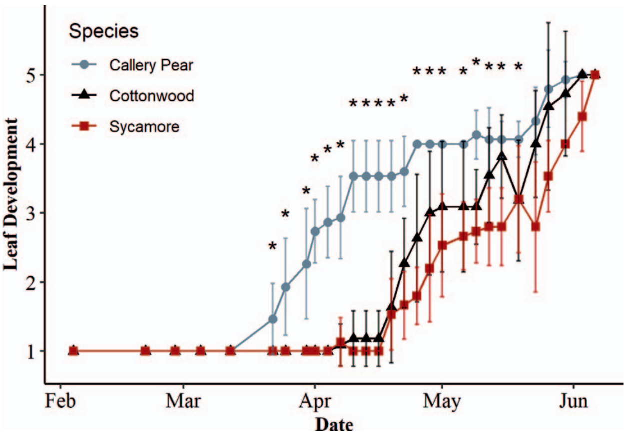

FIG. 1. Spring leaf development of an invasive tree, Callery pear (*Pyrus calleryana*), and the native tree species cottonwood (*Populus deltoides*) and sycamore (*Platanus occidentalis*) in southwest Ohio (mean ± 1 SD). Stars indicate statistical significance ($P < 0.001$) between values for *P. calleryana* and both native species. Dates are presented as three-letter codes for months on the *x*-axis. Leaf development was estimated on the basis of observations binned into the following leaf development categories: 1, bud dormant; 2, leaf blade visible; 3, entire leaf exposed; 4, entire leaf exposed and flat; 5, summer green.

2016). For the purposes of statistical analysis, the data were divided into spring (February 2, 2020 to May 6, 2020) and fall (July 7, 2020 to November 28, 2020) and repeated-measures analysis of variance (RMANOVA) was used to test for overall differences among species in each of these seasons using the lme4 package in R (Bates *et al*. 2015). After significant overall model effects, *post hoc* comparisons among species within each sampling date were made using pairwise *t*-tests with a Bonferroni correction. A 10-day period of unusually cold weather occurred in May 2020 and included subfreezing temperatures on May 9, 2020 (Supplemental Material, Fig. S1). This was the coldest temperature on record for this date in Dayton, OH (NWS 2022), and visual observations of the forests in the region indicated significant leaf damage across a range of species. Observations of leaf damage were made on May 11, 2020. Because data did not meet ANOVA assumptions, comparisons of leaf mortality among species were made using the Kruskal–Wallis rank-sum test followed by pairwise comparisons using the Wilcoxon rank-sum test and the *P*-value adjustment of Benjamini and Hochberg (1995).

Results. Leaf development of *Py. calleryana* began significantly earlier in the spring 2020 growing season than the native woody species (RMANOVA effect of species $P < 0.001$, Fig. 1). In March, *Py. calleryana* leaf blades became visible (leaf development category 2) and entire leaves were exposed (category 3) before *Po. deltoides* and *Pl. occidentalis* leaf blades were visible (Fig. 1). *Pyrus calleryana* was statistically distinguishable ($P < 0.001$) from both *Po. deltoides* and *Pl. occidentalis* from March 22, 2020 until May 23, 2020, indicating the potential for a 2-mo spring advantage in leaf development. Native tree leaf development was statistically indistinguishable during the spring growing season until a brief period from April 22, 2020 to April 28, 2020, when there was statistically significant separation in which *Py. calleryana* was more advanced than *Po. deltoides*, which was also more advanced than *Pl. occidentalis* (Fig. 1).

A late frost event in spring 2020 led to the opportunity to assess freeze tolerance in the study species. On May 9, 2022 the Dayton region experienced the coldest temperatures on record for that date (NWS 2022), including a low of –2.2 °C (USDC 2022b), which is much colder than average for Dayton (USDC 2022a; Supplemental Material, Fig. S1). This frost event differentially influenced the study species (Kruskal–Wallis $P < 0.001$), killing nearly all the leaves on *Pl. occidentalis* trees and 68% of *Po. deltoides* leaves (Fig. 2). *Pyrus calleryana* was left generally unaffected, averaging only 6% leaf mortality from the frost, which was significantly less than that of the native species ($P < 0.001$, Fig. 2). Because *Pl. occidentalis* had to effectively reinitiate leaf development and generate

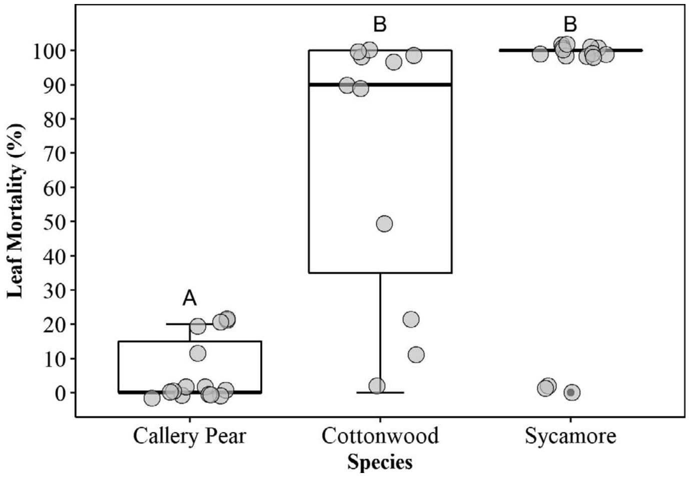

FIG. 2. Frost-related leaf mortality of an invasive tree, Callery pear (*Pyrus calleryana*), and the native tree species cottonwood (*Populus deltoides*) and sycamore (*Platanus occidentalis*) in southwest Ohio. Observations were made on May 11, 2020 and the damage was related to a cold snap and hard freeze event May 9, 2020 (Supplemental Material, Fig. S1). Statistical separation of the species is indicated by letters over the box plots (all $P < 0.001$). Center line of the box plots is the median value and points represent individual stems.

a new "flush" of leaves, the phenology of this species was delayed such that *Py. calleryana* and *Po. deltoides* had more advanced leaf phenology than *Pl. occidentalis* from May 23, 2020 to June 3, 2020 (Fig. 1).

In the fall, *Py. calleryana* retained its leaves for a longer duration than both *Po. deltoides* and *Pl. occidentalis* (RMANOVA effect of species $P < 0.001$, Fig. 3). From August 22, 2020 until November 6, 2020, *Py. calleryana* exhibited less of a transition toward senescence than both *Po. deltoides* and *Pl. occidentalis* (all; $P < 0.001$), whereas the native species were not statistically distinguishable except for September 18, 2020 when all three species were significantly different from one another (Fig. 3). Most notably, the leaves of *Pl. occidentalis* and *Po. deltoides* began to exhibit leaf coloration different from summer in early August (leaf development category 6) and were transitioning to full color change by the end

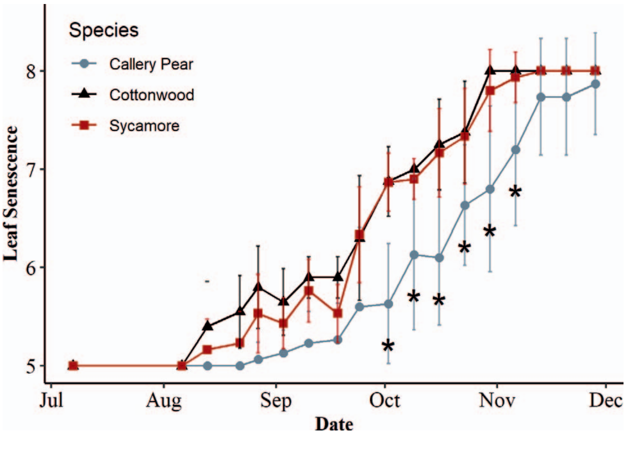

FIG. 3. Fall leaf development of an invasive tree, Callery pear (*Pyrus calleryana*), and the native tree species cottonwood (*Populus deltoides*) and sycamore (*Platanus occidentalis*) at three sites in southwest Ohio (mean ± 1 SD). Presence of stars indicate statistically detectable differences ($P < 0.001$) between values for *P. calleryana* and the two native species. Dates are presented as three-letter codes for months on the *x*-axis. Leaf senescence was estimated on the basis of observations binned into the following leaf development categories: 5, summer green; 6, leaf different from summer color; 7, leaf at fall color; 8, leaf abscission.

of September (category 7). *Pyrus calleryana* began to show colors different from summer green in late September but did not exhibit fall color until October (category 7). Most *Py. calleryana* trees did not reach full leaf abscission until November into December (Fig. 3).

Discussion. *Pyrus calleryana* is an invasive tree that has become particularly problematic in grasslands of the eastern USA because of a suite of traits that facilitate establishment of dense stands in open habitats. Woody invasive plants often exploit multiple mechanisms to outcompete species and dominate ecosystems and an extended leaf phenology has been noted in many invasive woody species (Xu *et al*. 2007, McEwan *et al*. 2009, Fridley 2012, Schuster and Dukes 2017). This extended phenology may provide an opportunity for carbon gain (Fridley 2012), although more work is needed to confirm this pattern. For example, recent work from O'Connell and Savage (2020) found that woody invasive plants retain leaves later than some native plants; however, this extended phenology was not necessarily associated with increased carbon gain when compared with native species. Our data suggest that *Py. calleryana* may have at least a 1-mo advantage in leaf duration in both spring and fall. Further research that confirms this pattern and provides an assessment of annual carbon gain relative to native competitors would advance understanding of the invasion biology of this important species.

Beyond the biological implications, the extended phenology of *Py. calleryana* may provide an opportunity for managers seeking to control this species. The visually obvious foliar displays in the spring and fall may allow for relative ease in locating this species in a matrix of native plants. Spring application of herbicide during a period when native leaves have yet to develop, while *Py. calleryana* have fully formed leaves, may allow for herbicide application with reduced potential for nontarget effects. Vogt *et al*. (2020) found nearly 100% mortality of *Py. calleryana* after application of different herbicides, and using the early phenology of this species to assist in targeting treatments may provide an advantage to land managers.

Frost tolerance may provide specific advantages to *Py. calleryana* during invasion of habitats in the eastern USA. The late frost event recorded in our study resulted in significant leaf mortality of both native species, whereas *Py. calleryana* leaf damage was visually undetectable and leaf development was seemingly unhindered. The particular physiological characteristics that enable this frost tolerance are presently unknown. Generally, plant frost tolerance is related to mechanisms that limit cell wall damage due to ice formation when the organism is exposed to cold temperatures (Nilsen 1992, Sakai and Larcher 2012, Takahashi *et al*. 2021). In our study, the frost tolerance of *Py. calleryana* both allowed this species to continue leaf development apace, presumably enabling a significant carbon acquisition advantage, and also enabled it to avoid the regrowth of leaf material that we observed in *Pl. occidentalis*. McEwan *et al*. (2009) found a similar pattern in the invasive shrub *L. maackii*—extended phenology and also greater frost tolerance than co-occurring native shrubs. The ability to withstand frost events may have implications for the potential northern expansion of the invasion front, which was thought to be potentially limited by winter temperatures (Culley and Hardiman 2007). Distributional limitations on invasive species such as *Py. calleryana* may be shifting through time because of climate change (Hellman *et al*. 2008). For example, Ikeda *et al*. (2014) found that *Tamarix* invasion will increase by 62% by 2080 because of warmer environments providing the opportunity for range expansion. Bradley *et al*. (2010) predicted that some important invasive plants in the eastern USA, including kudzu (*Pueraria lobata*), privet (*Ligustrum sinense*; *L. vulgare*), and cogongrass (*Imperata cylindrica*), will continue to expand their range because of the warming climate. More work is needed to understand the mechanism that enables freeze tolerance of invasive species like *Py. calleryana*, to connect this cold tolerance with adaptations that allow extended phenology, and to link those adaptations with the potential for range expansions that may be facilitated by climate warming (Bradley *et al*. 2010).

In summary, *Py. calleryana* had a much longer leaf phenology than the co-occurring native woody species *Pl. occidentalis* and *Po. deltoides*, with leaf out much earlier in spring and leaf drop much later in fall. *Pyrus calleryana* was seemingly invulnerable to a significant frost event that caused damage on both native species. The extended phenology may be useful to land managers seeking to control this species as it will allow application of herbicide when nontarget species foliage is absent and may create a visually obvious display for locating the species in a natural area. An extended leaf phenology in *Py. calleryana* may provide a significant competitive advantage to this species and can be considered one trait in a profile of characteristics that enable this species to be a problematic invader. Further work is required to elucidate the botanical mechanisms enabling this extended phenology and to link this ecological behavior with competitive advantage and the potential for range expansion into colder climates.

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