



## **Do multiple mechanisms drive the dominance of an invasive plant (*Ranunculus ficaria*, Ranunculaceae) along an urban stream? 1**

Authors: Masters, Jeffery A., and Emery, Sarah M.

Source: The Journal of the Torrey Botanical Society, 143(4) : 359-366

Published By: Torrey Botanical Society

URL: <https://doi.org/10.3159/TORREY-D-15-00020.1>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Do multiple mechanisms drive the dominance of an invasive plant (*Ranunculus ficaria*, Ranunculaceae) along an urban stream?<sup>1</sup>

Jeffery A. Masters<sup>2</sup> and Sarah M. Emery

Department of Biology, University of Louisville, Louisville, KY 40292

**Abstract.** Invasive plant species are believed to decrease biodiversity and local abundances of native species. Examining the mechanisms of invasive species impacts can help direct restoration efforts, especially where species employ multiple mechanisms to increase their relative dominance and negatively affect native species. *Ranunculus ficaria* is an invasive species in many temperate deciduous forests in the northeastern United States, and is especially dense in highly disturbed urban riparian habitats. This species may prevent establishment of native species in invaded areas directly through competition or allelopathy. Alternatively, its success may simply be a consequence of a modified disturbance regime. We tested for direct effects of *R. ficaria* on the growth of a native riparian grass phytometer, *Elymus riparius*. We also examined three potential mechanisms by which *R. ficaria* could directly impact native plants: nutrient competition, light/space competition, and allelopathy. We tested for nutrient competition by adding fertilizer to the soil in selected plots. To test for allelopathy, we added a tea made from *R. ficaria* leaves to selected plots. We also quantified plant community responses to *R. ficaria* removal based on volunteer seedling abundances. We found 99% higher phytometer biomass in removal plots than in invaded plots. Removal plots also had 493% more volunteer seedlings. There was no evidence for nutrient competition or allelopathy. *Ranunculus ficaria* is directly responsible for reducing volunteer sprout abundance and the biomass, but not necessarily diversity, in our study sites, probably through competition for space and/or light. This suggests that *R. ficaria* has some role in driving ecosystem change, and that removal of these populations will help restore some native species.

Key words: allelopathy, disturbance, driver-passenger model, *Elymus riparius*, *Ficaria verna*

Invasive plants are widely believed to decrease biodiversity and negatively impact native plants (Pimentel, Zuniga, and Morrison 2005). Aggressive invasive plants can impact species, communities, and entire ecosystems, but the direction and magnitude of these impacts also depend on the receiving system (Vila *et al.* 2011). Multiple environmental factors and species traits can contribute to the impacts of introduced plant species, and several mechanisms have been proposed to explain invasive plant success (Gurevitch and Padilla 2004, Didham *et al.* 2005, MacDougall and Turkington 2005). Many invasive plant species can directly outcompete native species for resources such as nutrients and light (Cipollini, McClain, and Cipollini 2008). Other invasive plants establish dominance via novel allelopathic properties, allowing them to directly

inhibit native plant growth (Callaway and Ridenour 2004, Callaway and Vivanco 2007). Still other invasive plants establish in disturbed habitats (Hobbs and Huenneke 1992, Jia *et al.* 2009), where dominance is due to the ability of the invading species to establish in areas that native species can no longer inhabit because of anthropogenic disturbance (Price *et al.* 2011). In other cases, the invading plant is a superior competitor in disturbed habitats and benefits from disturbance on the long term. For example, invasive *Rubus phoenicolasius* typically requires large treefall gaps in the canopy to become dominant; once established, populations persist even after the canopy has closed (Gorchov *et al.* 2011). From a management perspective, it is necessary to determine mechanisms of invasive plant dominance in order to effectively manage and restore invaded habitats. For example, while much invasive species management focuses on species removal efforts, if an underlying disturbance is responsible for the reduction in native species diversity, no amount of invasive removal will restore the plant community.

*Ranunculus ficaria* Huds. is an invasive species of low-lying wet areas in many temperate deciduous forests in the northeastern United States, and can be especially dense in urban riparian habitats. A perennial native to Europe and western Asia, it was first reported in the United States in

<sup>1</sup> The authors would like to thank Carl Cloyd, Cherise Montgomery, and Tommy Ross for field assistance and Louisville Olmsted Parks Conservancy for access to field sites.

<sup>2</sup> Author for correspondence: jeffery.masters@gmail.com

doi: 10.3159/TORREY-D-15-00020.1

©Copyright 2016 by The Torrey Botanical Society

Received for publication April 20, 2015, and in revised form October 28, 2015; first published August 1, 2016.

1867, and was probably introduced as an ornamental (Axtell, DiTommaso, and Post 2010). Invasive populations of *R. ficaria* have three modes of reproduction: seeds, bulbils, and tubers. Vegetative sprouts, which lack the fused, obcordate cotyledons of seedlings, can emerge as early as September. In spring, it forms thick mats of vegetation that appear to prevent establishment of other species in invaded areas through competition for light. It may also have some allelopathic properties (Cipollini and Schradin 2011). However, many of the riparian habitats dominated by *R. ficaria* are highly disturbed due to urbanization. Flash flooding and contaminant inundation from street runoff are frequent in these areas (Walsh *et al.* 2005), and its dominance may be due to the ability to tolerate this disturbance, rather than any inherent competitive advantage.

In this study, we tested for direct effects of *R. ficaria* on native plants in two different manipulative field experiments conducted in highly disturbed riparian habitats. We also examined three potential mechanisms by which *R. ficaria* could directly reduce native plant abundance: nutrient competition, light/space competition, and allelopathy. In particular, we asked the following questions: (a) Does *R. ficaria* directly reduce native plant abundance or do other factors, such as disturbance regime, maintain low diversity? (b) If *R. ficaria* does directly impact native plants, what is the potential mechanism? We hypothesized that presence of *R. ficaria* would have a negative effect on establishing species due to allelopathy and competition for light. Because urban flooding often increases soil nutrients, we did not expect competition for soil resources to be a significant mechanism of *R. ficaria* dominance. If our experimental manipulations had no effect on native plant abundance and diversity, we would interpret this as evidence that some other environmental parameter (*e.g.*, herbivory, anthropogenic disturbance) is the mechanism driving low species diversity and facilitating *R. ficaria* dominance.

**Materials and Methods.** **STUDY SITE.** We conducted our studies along Beargrass Creek (Middle Fork) in Cherokee Park (latitude 38.243301°N, longitude -85.698220°W), which is part of the Olmstead Parks system in Louisville, KY. The catchment in this area is urbanized and strongly channelized (approx. 33% impervious surface; Louisville and Jefferson County Metro-

politan Sewer District 2005), and the study sites are subject to flooding disturbance throughout the year, including street drainage and raw sewage overflow. Additionally, the area is heavily used by the public, including foot, pet, and mountain bike traffic. The riparian corridor is heavily invaded with *R. ficaria* (> 90% cover), which forms large monoculture patches at the study site from February to early April. There are some spring ephemerals such as *Claytonia virginica* L. and *Cardamine diphylla* Michx. that occur outside of the monoculture. However, the most common species at the study site other than *R. ficaria* are late spring and summer weedy species (*e.g.*, *Conyza canadensis* L., *Solidago canadensis* L., and *Sorghum halepense* L.). These species dominate the study site after *R. ficaria* has senesced.

**PILOT STUDY.** In early February 2012, we constructed five 2 × 0.75 m experimental blocks along a 25 m stretch of Beargrass Creek. Eight 25 × 25 cm plots were laid out within each block, and blocks were 3–10 m apart. We randomly applied treatment combinations (described below) to each plot, but only sampled a central 10 × 10 cm subplot within each plot, with the remainder of the plot acting as a buffer area between treatments. Treatment plots were kept relatively small for logistical reasons, as *R. ficaria* densities were very high (*e.g.*, 200–1,600 plants/m<sup>2</sup>).

Our treatment application followed a fully factorial block design with the following factors: Two *R. ficaria* removal levels (presence/absence) × 2 activated carbon levels (added/control) × 2 nutrient levels (added/control). Removal treatments tested whether *R. ficaria* presence directly inhibited native plant species. The activated carbon treatment evaluated whether allelopathy was a mechanism of inhibition, and the nutrient addition treatment tested whether competition for soil nutrients was a mechanism of inhibition.

For the removal treatment, we removed *R. ficaria* from the entire plot with careful digging. Removal was done by digging because tubers represent a significant store of energy for the plant and will continue to sprout if clipped. To standardize for the effects of soil disturbance, the soil in all plots were similarly disturbed by digging into the top 8 cm of soil around large *R. ficaria* plants and completely removing and replanting smaller plants. The soil disturbance in the uninvaded plots was to control for any unintentional effects of digging in the removal plots. While some

bulbil sprouts did not survive this process, larger individuals recovered quickly resulting in 100% cover of *R. ficaria* in all of the “*R. ficaria* present” plots. The density of *R. ficaria* individuals for the “*R. ficaria* present” plots ranged from 2 large plants per  $10 \times 10$  cm plot to 16 smaller individuals per plot. For the activated carbon addition treatment, we mixed 40 ml of activated carbon (dry measure; Aquarium Pharmaceuticals, API, Chalfont, PA) into the top 8 cm of soil. Activated carbon can absorb allelochemicals, and is frequently used in studies on allelopathy (Inderjit and Callaway 2003, Cipollini and Schradin 2011). For the nutrient addition treatment, we mixed 30 g of Osmocote (NPK 14-14-14; Scotts-Sierra Horticulture Products, Marysville, OH) into the top 8 cm of soil. On March 24, 2012, we counted all volunteer herbaceous sprouts and seedlings in the center  $10 \times 10$  cm area of each plot (excluding *R. ficaria* seedlings). The data were analyzed with a three-way blocked General Linear Model (GLM; SYSTAT v12, 2007; Systat Software, Inc., San Jose, CA) with *Ranunculus ficaria* removal, carbon addition, and nutrient addition as the main factors and block as a random variable. Response data were transformed,  $\ln(x + 1)$ , to meet test parameters.

We evaluated the importance of multiple mechanisms explaining the impacts of *Ranunculus ficaria* by examining the response of volunteer seedlings in each treatment plot. If nutrient competition was important, seedlings in invaded plots treated with nutrient addition would show a positive response relative to controls. If activated carbon addition in invaded plots had a positive effect on volunteer abundance, then we interpreted this as evidence that allelopathy was an important mechanism of *R. ficaria* dominance. Activated carbon can also have additional N and P, depending on the source (Lau *et al.* 2008), so nutrient addition also can serve as a control for the possible fertilization effects of carbon addition. If *R. ficaria* removal, but not nutrient or carbon additions, increased volunteer abundance, we interpreted this as evidence for direct competition for light and space between the invasive and establishing plants. If *R. ficaria* removal did not alter volunteer abundance, this would be evidence of other environmental factors such as herbivory, flooding, or a depauperate seed bank having overriding effects on the plant community.

PHYTOMETER EXPERIMENT. In the pilot study, no interactions were detected between treatments in the fully factorial model so we simplified the treatment application and the statistical model for the phytometer experiment, performed the following year. This allowed us to directly test for the effects of *R. ficaria* removal on native plants while still exploring the possible effects of nutrient competition and allelopathy. We designed a  $2 \times 3$  factorial experiment where *R. ficaria* presence or absence was crossed with three “mechanism” treatments to isolate potential mechanisms of native plant inhibition (fertilized, allelopathic extract, or control). Because of a possible confounding effect of activated carbon on nutrient availability in the pilot study, as well as possible lack of binding between allelochemicals and activated carbon, we also changed the method for testing allelopathic effects in the seed addition experiment using a tea made from *R. ficaria* leaves as a treatment (see Dorning and Cipollini 2006 for similar methods).

On February 11, 2013, 10 new blocks were established at least 3 m apart in areas where *R. ficaria* densities exceeded 90% ground cover. Blocks were  $1.25 \times 0.75$  m and contained six  $25 \times 25$  cm treatment plots separated by  $25 \times 25$  cm plots acting as buffer zones. *Ranunculus ficaria* individuals were removed from three randomly chosen plots in each block with careful digging. The soil in the three remaining plots was similarly disturbed to mimic the removal plots. To test whether nutrient competition was important, 75 g of Osmocote (Scotts-Sierra Horticulture Products) was mixed into the top 8 cm of soil of one removal treatment plot and one invaded plot in each block. To test whether allelopathy was important, a concentrated extract tea was made by soaking 400 g of dried *R. ficaria* leaves in 2 L of distilled water for 48 hr. This dried material was saved from the previous year to allow for an early season application of the extracts. Two-hundred ml of this tea was added to two treatment plots (one each of removal and invaded). The biomass used to create the concentration and final volume of extract applied to each plot approximated double the average dry weight biomass produced in  $25 \times 25$  cm reference plots. This treatment was also repeated later in the season as the plants began to flower. However, 1,000 g of fresh plant material per 2 L of water was prepared for the second application. To standardize for the effect of

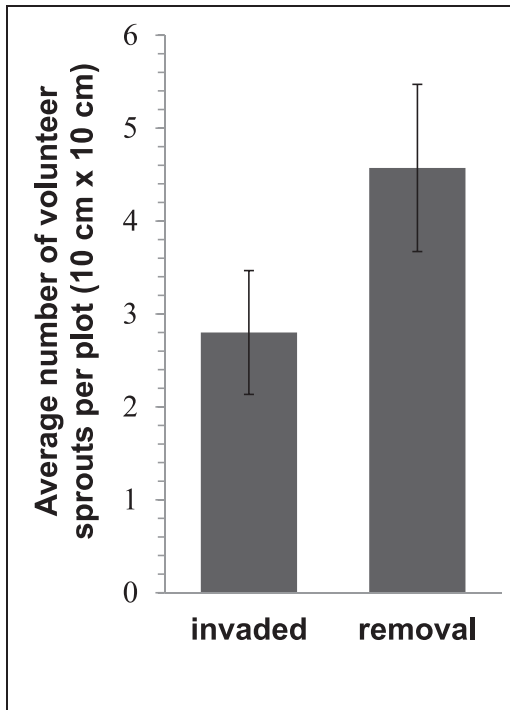


FIG. 1. Effects of *Ranunculus ficaria* removal on average volunteer sprout abundance, 2012 (pilot study). Error bars represent  $\pm 1$  SE.

watering the allelopathy plots, 200 ml of distilled water was added to the other treatment plots at the time of both field applications. The last two plots in each block were controls with no additional mechanism treatments beyond *R. ficaria* removal or presence. All treatment combinations were randomly assigned to plots within each block.

On February 25, 2013, approximately 1,000 (determined by weight) riverbank wild rye (*Elymus riparius*) seeds (Prairie Moon Nursery, Winona, MN) were added to each plot as a phytometer. This is a native, perennial grass species common in riparian areas and damp woodlands in Kentucky, but was not present at our study sites. On March 11, 2013, we counted *E. riparius* and all volunteer seedlings other than *R. ficaria*. Volunteer seedlings were assumed to originate from the existing seed bank or dispersal into our study plots. We were easily able to distinguish *E. riparius* seedlings from the volunteer seedlings. We harvested surviving *E. riparius* individuals on May 25, 2013, dried biomass at 60°C for 48 h, and weighed. The response data were analyzed with a two-way blocked GLM (SYSTAT v12, 2007), with

Table 1. Results of GLM for treatment effects on propagule abundance, 2012.

Source	Propagule abundance		
	d.f.	F	P
Removal	1	6.930	<b>0.011<sup>a</sup></b>
Carbon	1	0.092	0.763
Nutrient	1	0.561	0.457
Removal $\times$ Carbon	1	0.033	0.856
Removal $\times$ Nutrient	1	3.699	0.060
Carbon $\times$ Nutrient	1	1.619	0.209
Removal $\times$ Carbon $\times$ Nutrient	1	0.090	0.766
Block	1	48.942	<b>&lt; 0.001</b>

<sup>a</sup> Statistically significant results ( $P < 0.05$ ) are shown in bold.

*R. ficaria* removal and mechanism treatment as the main factors, and block as a random variable. The *E. riparius* biomass and volunteer seedling abundance data were transformed,  $\ln(x + 1)$ , to meet test parameters. We evaluated mechanisms of native plant inhibition by comparing emergence and growth of *E. riparius* and other native plants in different plots. If soil resources were important, then invaded nutrient addition plots should show a positive response for *E. riparius* and the volunteers, relative to controls. If the extract addition has a negative effect, then allelopathy may be an important factor. Direct competition for space (light) was assumed if there were no nutrient effects and if *E. riparius* and volunteer plants were more successful in *R. ficaria* removal plots compared with invaded plots.

**Results. PILOT STUDY.** In 2012, *R. ficaria* removal significantly influenced volunteer plant abundance, with 63% more volunteer seedlings in removal plots than invaded plots (Fig. 1, Table 1). There were also significant block effects for both response variables in 2012. No other significant effects from carbon addition, nutrient addition, or their interaction were detected (Table 1).

**PHYTOMETER EXPERIMENT.** In the 2013 experiment, *R. ficaria* removal significantly influenced final biomass of *E. riparius*, which was 99% greater in removal plots (Fig. 2A, Table 2). *Ranunculus ficaria* removal significantly increased volunteer sprout abundance, with an average of 493% more sprouts from other species in removal plots versus invaded plots in 2013 (Fig. 2B, Table 2). There were no significant effects detected from nutrient and extract additions on *E. riparius* biomass or sprout number, and no significant



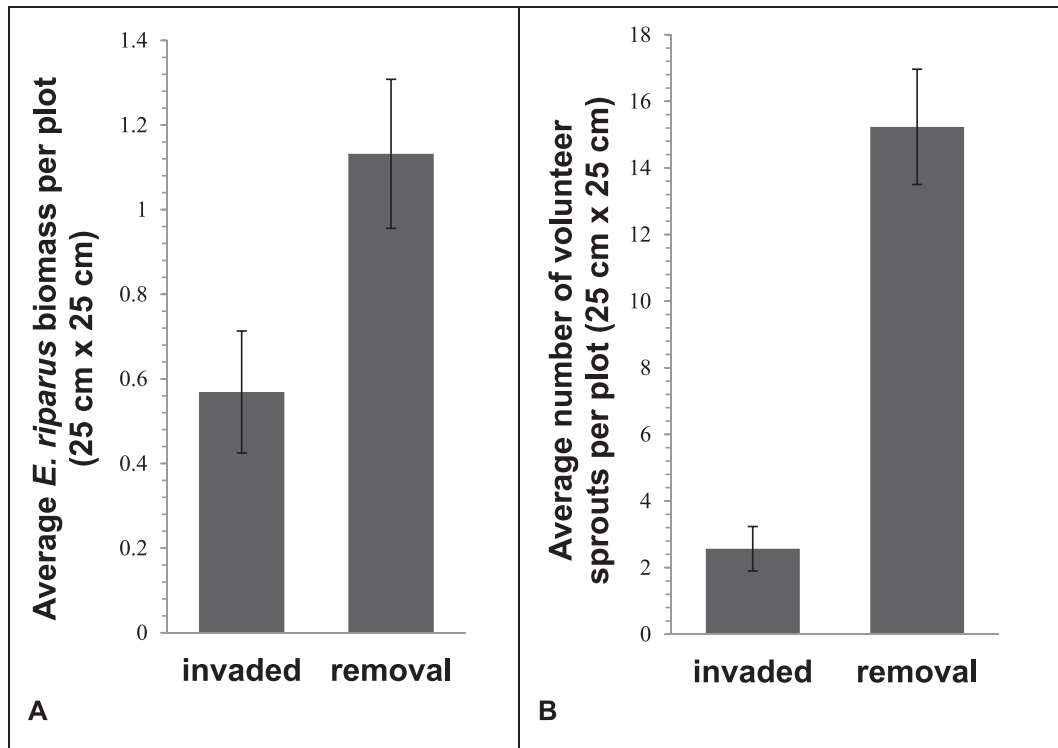


FIG. 2. Effects of *Ranunculus ficaria* removal on (A) *Elymus riparius* biomass and (B) average volunteer sprout (other than *E. riparius*) abundance per plot in 2013 (phytometer experiment). Error bars represent  $\pm$  SE.

effects detected on volunteer seedlings (Table 2). There were significant block effects on all response variables in 2013 (Table 2).

**Discussion.** Our results suggest that *R. ficaria* does have some direct negative effect on native plant communities, most likely through competition for space or light. Competition for space and light can be especially important if invasives emerge earlier in the growing season than native plants (Rejmanek 2013, Wainwright and Cleland 2013). For example, early emergence in garlic mustard (*Alliaria petiolata* Bieb.) contributes to a competitive advantage over native plants and

increased reproductive success (Engelhardt and Anderson 2011). *Ranunculus ficaria* emerges much earlier than other spring ephemerals and forms thick monocultures that likely crowd other species for space and/or light. Therefore, this early emergence may be a significant factor explaining this species' success and impacts on other species.

Nutrient additions did not have an effect on any response variable, suggesting that nutrient competition is not important in this system. Similarly, a previous study showed that nutrient additions had no effect on the native species *Impatiens capensis* in the presence of *R. ficaria* (Cipollini and Schradin 2011). As our study area is highly

Table 2. Results of GLM for *Ranunculus ficaria* removal and mechanism treatment effects on *Elymus riparius* sprout abundance, *E. riparius* biomass, and volunteer sprout abundance, 2013.

Source	<i>Elymus riparius</i> sprouts			<i>Elymus riparius</i> biomass			Volunteer sprout abundance		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
Removal	1	1.178	0.283	1	7.814	<b>0.007<sup>a</sup></b>	1	71.561	< <b>0.001</b>
Mechanism treatment	2	2.914	0.063	2	0.717	0.493	2	2.217	0.119
Removal $\times$ Mechanism	2	2.437	0.097	2	0.380	0.686	2	0.707	0.498
Block	1	20.143	< <b>0.001</b>	1	4.564	<b>0.037</b>	1	0.955	0.333

<sup>a</sup> Statistically significant results ( $P < 0.05$ ) are shown in bold.

disturbed from frequent urban flooding, the associated influx of nutrients (Walsh *et al.* 2005) may result in little nutrient limitation even in very dense populations. There was no heavy rainfall over the course of either experiment, but the study area was in a wet riparian corridor, and some nutrients may have been lost to leaching during smaller moisture events. We also conducted a soil analysis at the end of the experiment, sampling the overall amount of nutrients averaged across the fertilizer addition plots and the control plots (Appendix 1). Although fertilizer pellets were still visible in some nutrient addition plots (pellets were removed before soil analysis), there were no large differences in nutrients between the plots. This suggests that either urban flooding deposits an excess of nutrients in our study area, or that our treatments were simply not effective in creating differences over time, so our results concerning nutrient competition should be considered tentative.

We found no evidence for allelopathy as a mechanism of *R. ficaria* success in our study. Addition of carbon did not affect volunteer sprout numbers in the pilot experiment, and the addition of the extract did not affect any response variable in phytometer experiment. *Ranunculus ficaria* can negatively impact growth and reproduction of native plants through allelopathy, but this effect varies by target species (Cipollini and Schradin 2011), and *Elymus* may be tolerant to these allelochemicals. While other species of *Elymus* have shown sensitivity to allelopathic and volatile organic chemicals associated with anthropogenic disturbance (Beyschlag *et al.* 1996, Shang and Xu 2012, Zhang *et al.* 2012), the identities of the specific allelochemicals produced by *R. ficaria* are unknown and may not be active against the species of *Elymus* used in our experiment. Additionally, sensitivities (or lack thereof) of a single phytometer species may not be reflective of responses of the community as a whole. Alternatively, there are several caveats to our methodology in this study. We only applied the allelopathic tea twice, and the frequent urban flooding at our site could prevent the buildup of allelopathic chemicals. Also, in the first application, we used oven-dried material, which may have destroyed the allelopathic properties of the tea. Additionally, because our response variable was early sprout survival (and indirectly germination) in the surface soil, we only used above-ground biomass to make the tea. Most

of the below-ground growth throughout the season consists of perennial tubers, which may have lasting negative effects on the plant community not tested in this experiment. The potential allelopathic properties of this species merit additional study.

Invasive plants can be classified as drivers of ecosystem change or passengers benefitting from disturbance (MacDougall and Turkington 2005, Wilson and Pinno 2013). From a management perspective, invasive species that are passengers or drivers require different approaches for control. Directly reducing populations of invasive plants is important for species that are drivers, while controlling disturbance is more important for invasive plants that are passengers. Our results show that *R. ficaria* has some role in reducing other species abundance and diversity, probably through competition for light or space. This indicates a role in driving community change and suggests that direct management of these populations will help restore native diversity. Other unpublished data also suggest that *R. ficaria* can reduce native plant abundance and species richness in invaded habitats (Hohman 2005); however, the importance of disturbance in this system cannot be ruled out. Some of our results (no nutrient competition or allelopathic effects detected) could be explained by the effects of urban flooding. In addition, many native species are known to be intolerant to the flash flooding associated with urban hydrology (Meyer, Paul, and Taulbee 2005, Walsh *et al.* 2005). It is likely that this species follows the “back-seat driver” model (Bauer 2012), exhibiting superior competitive abilities but also benefitting from reduced competition in disturbed habitats. Further study of this species as a passenger is needed to determine its entire role in community change.

#### Literature Cited

- AXTELL, A. E., A. DiTOMMASO, AND A. R. POST. 2010. Lesser celandine (*Ranunculus ficaria*): A threat to woodland habitats in the northern United States and southern Canada. *Invasive Plant Science and Management* 3: 190–196.
- BAUER, J. T. 2012. Invasive species: “back-seat drivers” of ecosystem change? *Biol. Invasions* 14: 1295–1304.
- BEYSCHLAG, W., R. J. RYEL, I. ULLMANN, AND J. ECKSTEIN. 1996. Experimental studies on the competitive balance between two central European roadside grasses with different growth forms. 2. Controlled experiments on the influence of soil depth, salinity, and allelopathy. *Botanica Acta* 109: 449–455.
- CALLAWAY, R. M. AND W. M. RIDENOUR. 2004. Novel weapons: invasive success and the evolution of

- increased competitive ability. *Frontiers in Ecology and the Environment* 2: 436–443.
- CALLAWAY, R. M. AND J. M. VIVANCO. 2007. Invasion of plants into native communities using the underground information superhighway. *Allelopath. J.* 19: 143–151.
- CIPOLLINI, K. A. AND K. D. SCHRADIN. 2011. Guilty in the court of public opinion: testing presumptive impacts and allelopathic potential of *Ranunculus ficaria*. *Am. Midl. Nat.* 166: 63–74.
- CIPOLLINI, K. A., G. Y. MCCLAIN, AND D. CIPOLLINI. 2008. Separating above- and belowground effects of *Alliaria petiolata* and *Lonicera maackii* on the performance of *Impatiens capensis*. *Am. Midl. Nat.* 160: 117–128.
- DORNING, M., AND D. CIPOLLINI. 2006. Leaf and root extracts of the invasive shrub, *Lonicera maackii*, inhibit seed germination of three herbs with no autotoxic effects. *Plant Ecol.* 184: 287–296.
- DIDHAM, R. K., J. M. TYLIANAKIS, M. A. HUTCHISON, R. M. EWERS, AND N. J. GEMMELL. 2005. Are invasive species the drivers of ecological change? *Trends Ecol. Evol.* 20: 470–474.
- ENGELHARDT, M. J. AND R. C. ANDERSON. 2011. Phenological niche separation from native species increases reproductive success of an invasive species: *Alliaria petiolata* (Brassicaceae)—garlic mustard. *J. Torrey Bot. Soc.* 138: 418–433.
- GORCHOV D. L., E. THOMPSON, J. O'NEILL, D. WHIGHAM, AND D. A. NOE. 2011. Treefall gaps required for establishment, but not survival, of invasive *Rubus phoenicolasius* in deciduous forest, Maryland, USA. *Plant Spec. Biol.* 26: 221–223.
- GUREVITCH, J. AND D. K. PADILLA. 2004. Are invasive species a major cause of extinctions? *Trends Ecol. Evol.* 19: 470–474.
- HOBBS, R. J. AND L. F. HUENNEKE. 1992. Disturbance, diversity, and invasion: implications for conservations. *Conserv. Biol.* 6: 324–337.
- HOHMAN, B. M. 2005. *Ranunculus ficaria* L. tuber production and differences in community structure associated with its invasion and removal. M.S. thesis, Wright State University, Dayton, OH.
- INDERJIT AND R. M. CALLAWAY. 2003. Experimental designs for the study of allelopathy. *Plant Soil* 256: 1–11.
- JIA, X., X. Y. PAN, B. LI, J. K. CHEN, AND X. Z. YANG. 2009. Allometric growth, disturbance regime, and dilemmas of controlling invasive plants: a model analysis. *Biol. Invasions* 11: 743–752.
- LAU, J. A., K. P. PULIAFICO, J. A. KOPSHEVER, H. STELTZER, E. P. JARVIS, M. SCHWARZLANDER, S. Y. STRAUSS, AND R. A. HUFBAUER. 2008. Inference of allelopathy is complicated by effects of activated carbon on plant growth. *New Phytol.* 178: 412–423.
- LOUISVILLE AND JEFFERSON COUNTY METROPOLITAN SEWER DISTRICT (MSD). 2005. Beargrass Creek Watershed: State of the Streams. Louisville and Jefferson County MSD, Louisville, KY.
- MACDOUGALL, A. S. AND R. TURKINGTON. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86: 42–55.
- MEYER, J. L., M. J. PAUL, AND W. K. TAULBEE. 2005. Stream ecosystem function in urbanizing landscapes. *J. North Am. Benthol. Soc.* 24: 602–612.
- PIMENTEL, D., R. ZUNIGA, AND D. MORRISON. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* 52: 273–288.
- PRICE, J. N., P. J. BERNEY, D. RYDER, R. D. B. WHALLEY, AND C. L. GROSS. 2011. Disturbance governs dominance of an invasive forb in a temporary wetland. *Oecologia* 167: 759–769.
- REJMANEK, M. 2013. Extended leaf phenology: a secret of successful invaders? *J. Veg. Sci.* 24: 975–976.
- SHANG, Z. H. AND S. G. XU. 2012. Allelopathic testing of *Pedicularis kansuensis* (Scrophulariaceae) on seed germination and seedling growth of two native grasses in the Tibetan plateau. *Phyton (B. Aires)* 81: 75–79.
- SYSTAT v12. 2007. SYSTAT Software Inc., Chicago, IL.
- VILA, M., J. L. ESPINAR, M. HEJDA, P. E. HULME, V. JAROSIK, J. L. MARON, J. PERGL, U. SCHAFFNER, Y. SUN, AND P. PYSEK. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14: 702–770.
- WAINWRIGHT, C. E. AND E. E. CLELAND. 2013. Exotic species display greater germination plasticity and higher germination rates than native species across multiple cues. *Biol. Invasions* 15: 2253–2264.
- WALSH, C. J., A. H. ROY, J. W. FEMINELLA, P. D. COTTINGHAM, P. M. GROFFMAN, AND R. P. MORGAN. 2005. The urban stream syndrome: current knowledge and the search for a cure. *J. North Am. Benthol. Soc.* 24: 706–723.
- WILSON, S. D. AND B. D. PINNO. 2013. Environmentally-contingent behaviour of invasive plants as drivers or passengers. *Oikos* 122: 129–135.
- ZHANG, R. M., Z. J. ZUO, P. J. GAO, R. HOU, G. S. WEN, AND Y. GAO. 2012. Allelopathic effects of VOCs of *Artemisia frigida* Willd. on the regeneration of pasture grasses in Inner Mongolia. *J. Arid Environ.* 87: 212–218.



**APPENDIX**

Soil parameters in control plots (no removal or additions) and nutrient addition plots. To obtain soil samples, 0.5 L of soil (dry measure) was collected from each control plot and each nutrient addition plot at the end of the seed addition experiment. The soils for each treatment were combined then sent to the University of Kentucky Soil Testing Laboratory for analysis.

	Control plots (no treatments)	Nutrient addition plots
Organic matter (%)	5.80	6.05
Total nitrogen (%)	0.287	0.311
Phosphorus (ppm)	176	171
Potassium (ppm)	280	319
Soil pH	7.6	7.4
Calcium (ppm)	7,600	6,489
Magnesium (ppm)	728	639
Zinc (ppm)	58.3	51.1