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Allelopathic invasive tree (*Rhamnus cathartica*) alters native plant communities

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Abstract Many plants release allelopathic chemicals that can inhibit germination, growth, and/or survival in neighboring plants. These impacts appear magnified with the invasion of some non-native plants which may produce allelochemicals against which native fauna have not co-evolved resistance. Our objective was to examine the potential allelopathic impact of an invasive non-native shrub/tree on multiple plant species using field observation and experimental allelopathy studies. We surveyed and collected an invasive, non-native tree/shrub (*Rhamnus cathartica*) at Tifft Nature Preserve (a 107-ha urban natural area near Lake Erie in Buffalo, NY). We also surveyed understory plant communities in the urban forest to examine correlations between *R. cathartica* abundance and local plant community abundance and richness. We then used experimental mesocosms to test if patterns observed in the field could be explained by adding increased dosages of *R. cathartica* to soils containing five plant species, including native and non-native woody and herbaceous species. In the highly invaded urban forest, we found that herbaceous cover, shrubs and woody seedlings negatively covaried with *R. cathartica* basal area and seedlings density. In the mesocosm experiments, *R. cathartica* resulted in significant decreases in plant community species richness, abundance, and shifted biomass allocation from roots. Our results provide evidence that *R. cathartica* is highly allelopathic in its invaded range, that *R. cathartica* roots have an allelopathic effect and that some plant species appear immune. We suggest that these effects may explain the plant's ability to form dense monocultures and resist competitors, as well as shift community composition with species-specific impacts.

Keywords Allelopathy · Phytotoxicity · Recruitment · Urban ecology

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Introduction

Plants release secondary chemical compounds (not essential for growth, reproduction, and survival) that deter and inhibit herbivores and other plants; the deleterious effect on other plants is called allelopathy (Rice 1984). Allelopathic plants release phytotoxic chemicals into the soil environment through root and leaf leachate that can inhibit the germination, growth, and/or survival of neighboring plants (Fernandez et al. 2016; Lankau 2011; Orr et al. 2005). Some invasive plants appear to gain considerable advantage in novel ecosystems because they produce phytotoxic allelochemicals against which invaded-range native species may not have co-evolved resistance (Callaway and Ridenour 2004; Fernandez et al. 2016; Pisula and Meiners 2010; Thorpe et al. 2009). As a result, some invasive plants may form dense monocultures where native plants cannot compete well.

European or common buckthorn (*Rhamnus cathartica* L.) is a shrub/small tree native to most of Europe and Western Asia that appears restricted to open and edge habitats in its native range but is able to invade forest understories and dominate native ecosystems which were introduced in northern North America (Knight et al. 2007; Kurylo and Endress 2012). The shrub forms dense thickets that correspond with noticeable declines in native plant abundance and diversity (Archibold et al. 1997; Boudreau and Wilson 1992; Mascaro and Schnitzer 2007). The cause and effect between *R. cathartica* and native plant communities remains unclear, however, as the shrub appears as an opportunist, which employs multiple potential competitive mechanisms. *Rhamnus cathartica* tolerates a poor habitat (e.g., dry, shady), and it germinates, grows and reproduces vigorously in disturbed habitats where sunlight is plentiful (Gavier-Pizarro et al. 2010; Knight et al. 2007; Moffatt and McLachlan 2004). Still, *R. cathartica* invasion success may not be just opportunistic. The shrub leafs out earlier and thus is able to photosynthesize longer than co-occurring native species, allowing invasion into canopy understory, and it produces copious seed-bearing fruits that are dispersed by birds and mammals (Godwin 1936; Harrington et al. 1989).

Rhamnus cathartica also produces secondary compounds that alter soil chemistry, deter native herbivores, and appear to suppress native flora and fauna (Grunzweig et al. 2015; Heneghan et al. 2006; Klionsky et al. 2011; Schuh and Larsen 2015; Seltzner and Eddy 2003; Trial Jr. and Diamond 1979). In particular, phytotoxic compounds leached from the bark, leaves, stems and fruit—including emodin and other anthraquinones, tannins, and flavonoids (*see* Izhaki 2002 *and references therein*)—may suppress the germination, survival and growth of other plants (Archibold et al. 1997; Klionsky et al. 2011; Seltzner and Eddy 2003), though these effects require substantiation (Knight et al. 2007). *Rhamnus cathartica* leaves and fruit demonstrably reduced germination in some native and ornamental species, but *R. cathartica* bark and roots did not, and the effects appeared species specific (Klionsky et al. 2011; Knight et al. 2007). Hence, *R. cathartica* allelopathic effects may depend on its tissue type, and the effectiveness may depend on the identity and life stage of the target species.

Our objective was to examine the allelopathic impact of an invasive non-native shrub/tree on plant species using field observation and experimental allelopathy studies. Given the known allelochemical content, and predicted allelopathic effects, of *R. cathartica*, we predicted that increased soil amendments with *R. cathartica* leaf and root tissues would inhibit plant germination and growth in five woody and herbaceous plant species.

Methods

Study site

The Tifft Nature Preserve is a 107-ha urban natural area located on the shore of Lake Erie in Buffalo, NY (U.S.). The landscape was used for industrial and residential refuse, and turned into a natural area in the 1970s. The preserve contains deciduous forest (dominated by *Populus deltoides* W. Bartram ex Marshall), wetlands, and open fields.

Forest survey data collection

Herbaceous and woody plants were surveyed in the Tifft woodlands and grasslands in August 2013. Three random transects were established in each of these two habitats ($n = 6$ transects); all were 500 m long except one woodland transect which was 250 m long due to forest shape. Plots were established at 50-m intervals ($n = 55$ plots). Areas with active management and edges were avoided by moving plots 50 m. Total herbaceous percent cover and species richness, as well as woody seedlings (<1 cm dbh), were measured in 1 m^2 subplots ($n = 55$). For woody species, each plot was sampled using the point-center quarter technique ($n = 51$, Cottam and Curtis 1956) at the same 50-m intervals along the transects. Point-center quarter is a long-used forest sampling protocol in which a random point is selected, a compass used to divide the area into quadrants and the nearest tree (>11.7 cm dbh) and shrub (<11.7 cm dbh) located, and identified, and dbh (stem diameter at 1.4 m height) measured in each quadrant.

Forest survey data analysis

We examined 1-m^2-subplot-level variation among herbaceous cover (%) and herbaceous species richness, and point-quarter-plot-level tree richness, shrub richness, woody seedling density (stems · m^{-2}), *R. cathartica* basal area (stem basal area * stem density), tree basal area, shrub basal area, and *R. cathartica* basal area using principal component analysis (PCA) using the "prcomp" method and "scale" option (standardizes all variables to unit length) in the "R" statistical package (R Development Core Team 2016).

Mesocosm experimental design

Rhamnus cathartica leaves and roots were haphazardly collected at Tifft in September 2015 by removing whole plants <2.5 cm DBH, which were stored at 15 °C before being prepared for the mesocosm experiments. In January 2016, the *R. cathartica* plant material was placed in a drying oven for 7 days at 15 °C. The plant material was macerated and mixed with soil in one of four treatments: 0.1 g leaf, 1 g leaf, 10 g leaf, and 5 g root. Fifty mesocosms (12.5 cm clay pots) were filled with 250 g of sterile potting soil and planted with 10 seeds of each of 5 plant species (*Pinus strobus* L, *P. deltoides*, *Microstegium vimineum* (Trin.) A. Camus, *Liatris cylindracea* Michx., *Symphyotrichum oolentangiense* (Riddell) G.L. Nesom). These are a combination of herbaceous (*M. vimineum*, *L. cylindracea*, *S. oolentangiense*) and woody (*P. strobus*, *P. deltoides*) plants, including a plant from Asia (*M. vimineum*) that is invasive in North America and generally occurs in open to partly shady conditions (and hence could compete with *R. cathartica* in disturbed habitat). *Pinus strobus* and *P. deltoides* seeds were purchased from Sheffield's Seed Company (Locke, NY USA); *L. cylindracea* and *S. oolentangiense* seeds were purchased from Prairie Moon Nursery (Winona, MN USA). *Microstegium vimineum* seeds were collected from wild populations in Otto, NC (USA) in 2013 and stored in a dry cabinet. The *P. strobus, S. oolentangiense*, and *L. cylindracea* seeds were cold stratified at 4.5 °C for 60 days; the other seeds were not cold stratified.

Ten mesocosms were designated for each of the four treatments (and a control) [$n = 50$ total]. The mesocosms were placed under full spectrum growth lights and warmed to 21.5 °C using seed heating pads to encourage germination. The location of each mesocosm was randomized and shifted under different grow lights once per week. After 12 weeks, all plants were harvested, above- and belowground matter separated, and dried for 3 days at 15 °C before weighing. The species that germinated survived until the end of the experiment.

Mesocosm data analysis

We evaluated the *R. cathartica* treatment effects (0.1 g leaf, 1 g leaf, 10 g leaf, 5 g root) on mesocosm species richness, recruitment (seedling abundance), biomass (biomass · total seedlings^{-1}), and root:shoot ratio using analysis of variance (ANOVA) models in the R statistical program (R Development Core Team 2016). We used Tukey's HSD for post hoc evaluation of the differences in terms. In the root:shoot model, we included belowground biomass as the dependent variable and aboveground biomass as a predictor along with the treatment levels. We included an aboveground biomass × treatment interaction term to analyze how the ratio may vary by treatment level.

We also examined species-specific recruitment success (germinated · planted^{-1}) by *R. cathartica* treatment (and species × treatment interaction) using ANOVA.

Results

Field surveys

Herbaceous cover at Tifft was 87.3 ± 4% m^{-2} (mean ± SE) and herbaceous richness 2.5 ± 0.2% m^{-2}. The most common understory species were non-native plants (*R. cathartica*, *Polygonum cuspidatum* Siebold & Zucc., and *Phragmites* spp.) and some native *Urtica dioica* L. and *Solidago* spp. Woody seedling abundance was 0.6 ± 0.2 stems m^{-2}, and *R. cathartica* seedling abundance was 1.7 ± 0.4 stems m^{-2}. *Rhamnus cathartica* generally occurred as a large shrub/small tree (9.4 ± 0.5 dbh) at Tifft and dominated the understory (relative density; 257 stems · ha^{-1}). Co-occurring shrubs included *Cornus racemosa* Lam. and *Rhus typhina* L., but they were a fraction (combined = 33 stems · ha^{-1}) of the *R. cathartica*-dominated layer. *Populus deltoides* trees dominated the canopy layer (175 stems · ha^{-1}) and were much larger (92.1 ± 4.5 cm dbh) than *R. cathartica*. *Rhamnus cathartica* was more widespread in the forested (459 stems · ha^{-1}) than grassy (56 stems · ha^{-1}) habitats.

The field survey PCA indicated that most variation (34%) occurred along the PC1 axis where herbaceous cover negatively covaried with tree basal area and woody and *R. cathartica* seedling abundances (Fig. 1). We used the minimum contribution if all variable loadings contributed equally (38% here) to determine the most important loadings for each principle component. These loadings indicated that the most important PC1 components were percent herbaceous cover (−0.472) which negatively covaried with *R cathartica* seedling (0.416) and other woody seedling density (0.448). On PC2, however, the most important components were *R. cathartica* basal area (−0.525) and seedling density (−0.393), which negatively covaried with shrub basal area (0.443) and woody seedling density (0.418).

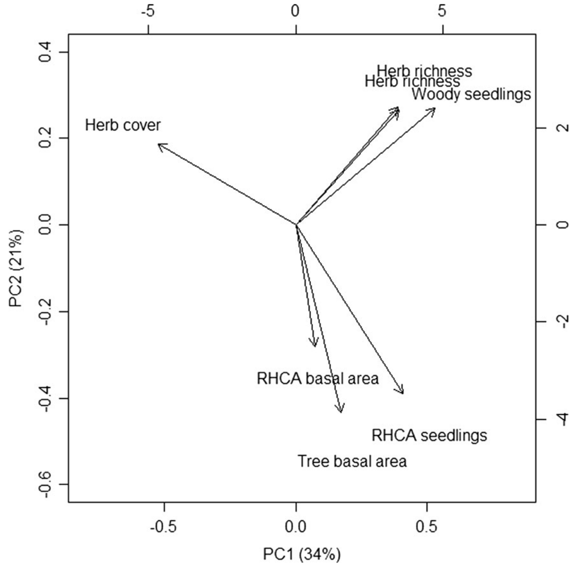

Fig. 1 Principal component analysis of plot-level variation in herbaceous coverage (herb cover) and species richness (herb richness), native woody basal area (shrub and tree area) and species richness (shrub and tree richness), native shrub and tree seedlings (woody seedlings) and *Rhamnus cathartica* basal area (RHCA area) and seedlings (RHCA seedlings). *Arrows* pointing in the same direction indicate positive covariation and those pointing in opposite directions indicate negative covariation. The component loadings indicated that the most important PC1 components (*horizontal axis*) were percent herbaceous cover, which negatively covaried with *R cathartica* and other woody seedling density. On PC2 (*vertical axis*), the most important components were *R. cathartica* basal area and seedling density, which negatively covaried with shrub basal area and woody seedling density

Mesocosm experiment

Overall, mesocosm recruitment was 11.6%. *Pinus strobus* had the highest recruitment rate with 22.6% of the seeds germinating and surviving. *Liatris cylindracea* also had a high recruitment rate at 20.0% followed by *P. deltoides* at 11.8%. Recruitment was low for *S. oolentangiense* (3.6%) and very low for *M. vimineum* (0.4%).

Mesocosm species richness differed significantly with *R. cathartica* treatments with a clear decline in response to increased dosage (Table 1a; Fig. 2a). The declines in species richness between the lowest leaf amendment (0.1 g) and control, and between the highest leaf amendment (10 g) and root amendments, did not differ, but the decline across all amendments with increased *R. cathartica* formed a clear negative trend. Species abundance also differed significantly with *R. cathartica* treatments, but the decline in response to dosage was not as consistent as species richness (Table 1b; Fig. 2b). Species abundance was significantly less in all of the *R. cathartica* treatments than the control; however, the two lowest amendments (0.1 and 1 g) did not differ, nor did the highest dosage (10 g) and root amendment.

Biomass seedling^{-1} did not significantly differ among treatments (Table 1c; Fig. 2c). A significant aboveground biomass × treatment interaction term indicated that the root:shoot ratio (belowground:aboveground biomass) differed by treatment (Table 1d; Fig. 3). The control and low dosage *R. cathartica* treatment ratios were quite similar with a relatively constant root:shoot ratio indicating that biomass was allocated relatively equally as the plants grew. However, at higher *R. cathartica* doses, the plants allocated considerably more biomass to shoots than roots.

Table 1 Analysis of variance for mesocosm plant community (a) species richness, (b) abundance, (c) biomass (d) belowground biomass, and (e) recruitment

Variable	*Df*	*SS*	*MS*	*f-value*	*p value*
A. Species richness					
Treatment	4	66.32	16.58	46.63	<0.001
Residuals	45	16.00	0.36		
B. Abundance					
Treatment	4	476.50	119.13	19.70	<0.001
Residuals	45	272.20	6.05		
C. Biomass					
Treatment	4	14,605	3651	0.91	0.468
Residuals	45	172,957	4022		
D. Root: shoot (belowground biomass)					
Aboveground biomass	1	0.00022	0.00022	12.806	<0.001
Treatment	4	0.00031	0.00008	4.535	0.004
Interaction		0.00024	0.00006	3.596	0.013
Residuals	45	0.00064	0.00002		
E. Species-specific recruitment					
Treatment	4	95.3	23.83	29.676	<0.001
Species	4	189.2	47.29	58.904	<0.001
Interaction	16	119.8	7.49	9.328	<0.001
Residuals	225	180.7	0.80		

Rhamnus cathartica treatments were as follows: control, 0.1 g leaf, 1 g leaf, 10 g leaf, and 5 g root. The root:shoot ratio was analyzed using belowground biomass as the dependent variable and aboveground biomass as an independent variable. The treatment × aboveground biomass interaction term indicated if biomass allocation shifted with treatment

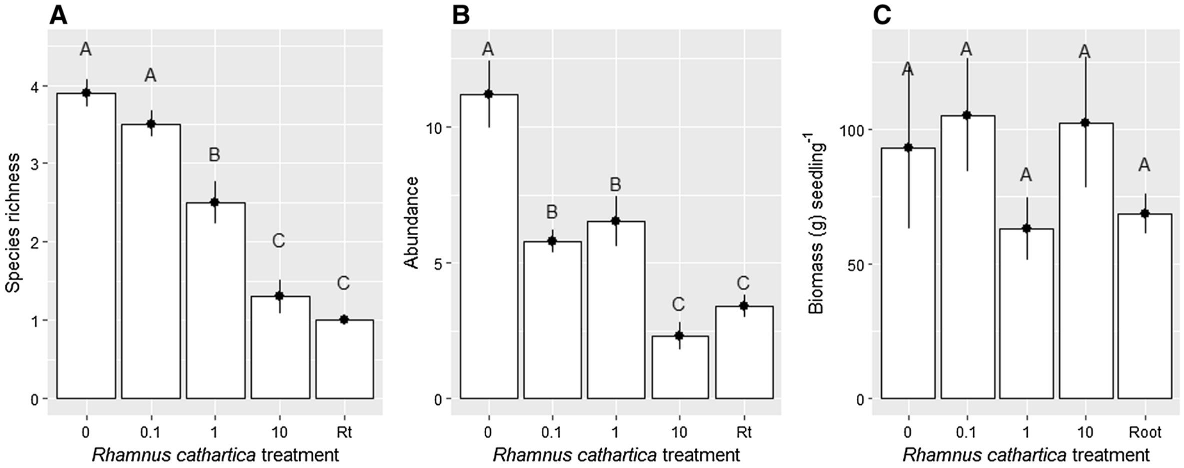

Fig. 2 *Rhamnus cathartica* treatment effects (control [0], 0.1 g leaf [0.1], 1 g leaf [1], 10 g leaf [10] and 5 g root [Rt]) on mesocosm species richness (**a**), abundance (**b**) and biomass (**c**). Statistically different treatments are labelled with *different letters*. *Error bars* indicate mean ± SE

A significant species × treatment interaction term indicated species-specific treatment responses (Table 1e; Fig. 4). *Microstegium vimineum* had particularly low germination in this study, and it only germinated in the control and lowest *R. cathartica* dosage mesocosms. *Populus deltoides*, *L. cylindracea*, and *S. oolentangiense* recruitment all decreased with increased *R. carthartica* dosages (with root being the 'highest' dosage); *Populus deltoides* appeared the most impacted as it only germinated in the control and lowest *R. cathartica* dosage mesocosms. *Pinus strobus* was the anomaly as it seemed only slightly negatively impacted by *R. cathartica* leaf additions, unaffected

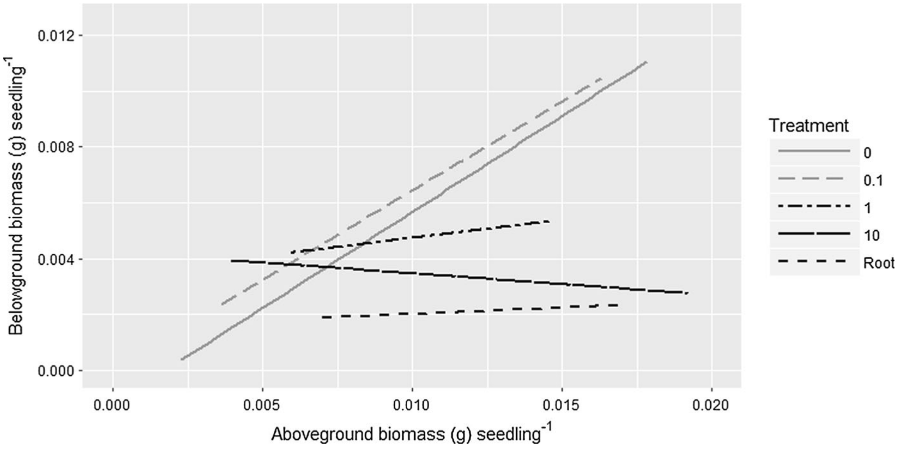

Fig. 3 Biomass allocation interaction plot with ratio between above- and belowground as function of the *Rhamnus cathartica* treatments (control [0], 0.1 g leaf [0.1], 1 g leaf [1], 10 g leaf [10] and 5 g root [Rt])

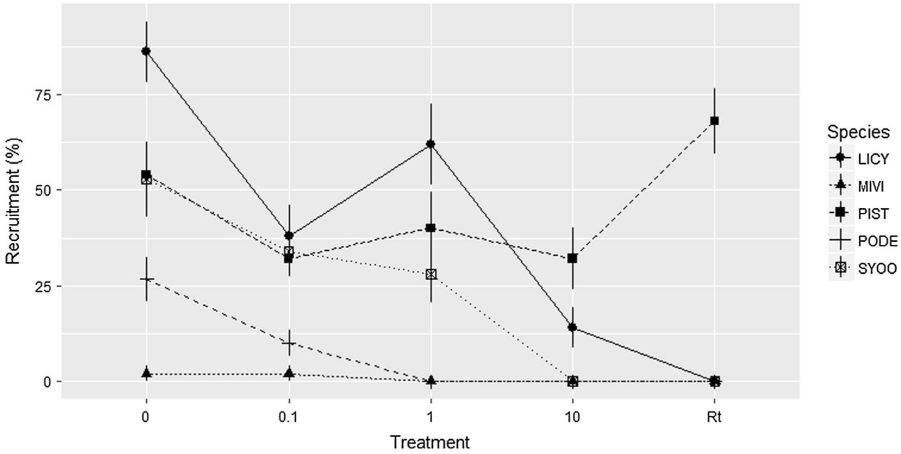

Fig. 4 Species × treatment interaction plot for plant seedling recruitment [*Pinus strobus* (PIST), *Populus deltoides* (PODE), *Microstegium vimineum* (MIVI), *Liatris cylindracea* (LICY) and *Symphyotrichum oolentangiense* (SYOO)], and *Rhamnus cathartica* treatments (control [0], 0.1 g leaf [0.1], 1 g leaf [1], 10 g leaf [10] and 5 g root [Rt])

by increased leaf dosage, and it actually improved germination with root addition.

Discussion

Rhamnus cathartica leaf and root tissue alone appeared sufficient to inhibit potential plant competitors and shift local plant community succession—suggesting an allelochemical mechanism. We found a negative relationship between *R. cathartica* and herbaceous- and shrub-layer plants in a highly invaded landscape that could indicate that *R. cathartica* outcompeted the other plants or took advantage of habitat disturbance and/or co-occurring non-native facilitators. Mesocosm experiments were far less ambiguous: increased doses of *R. cathartica* soil amendments resulted in significantly decreased plant community species richness and abundance, and a shift in biomass allocation from roots and shoots. Moreover, the *R. cathartica* impacts appeared species specific as the study plants differed in their sensitivities to *R. cathartica* soil amendments.

Our field surveys showing *R. cathartica*'s dominance beneath the canopy trees are consistent with several other studies in northeastern North America that report the plant in dense monocultures devoid of similarly sized woody plants or an appreciable herbaceous layer (Archibold et al. 1997; Boudreau and Wilson 1992; Mascaro and Schnitzer 2007). *Rhamnus cathartica* occurs in both sunny and shady habitats, appearing to favor sunny areas (Gavier-Pizarro et al.

2010; Moffatt and McLachlan 2004), but we found it far more extensively beneath canopy trees than in open grassy habitats. Given that the canopy trees at Tifft are mostly *P. deltoides*, a fast-growing tree associated with habitat disturbance, and *R. cathartica* also is associated with disturbance, it is likely that both were established when the Tifft landscape reverted from its industrial use in the 1970s. Once established, *R. cathartica* has many traits that could help it compete against other plants, such as low rates of herbivore attack, a thick, shading canopy, fast growth and reproduction, and an extended phenology allowing relatively greater carbon gain (Knight et al. 2007). We show that allelopathy also may be a key component of its competitive ability.

We targeted *R. cathartica* allelopathy as one explanation for the plant's community level effects. We used five wild plant species (four native and one non-native, two woody and three perennials) to examine the potential community-level effects in the mesocosms, and we found that increased *R. cathartica* leaf soil amendments, with a root amendment showing the most impact, reduced plant richness, and abundance. Interestingly, biomass · seedling^{-1} did not change with *R. cathartica* amendments for those plants that germinated, but biomass allocation did. In no- or low-dose *R. cathartica* treatments, plants allocated about the same biomass to above- and below-ground tissues regardless of size. In higher-dose *R. cathartica* treatments, biomass allocation was disproportionally shifted aboveground. The biomass shift could be a response to allelopathic chemicals in the soil, but also might have been prompted by the high level of nitrogen typically found in *R. cathartica* leaves (Harrington et al. 1989). That said, the biomass allocation response was similar between the highest leaf amendment and the root amendment, which would likely introduce different levels of nitrogen from *R. cathartica*, and increased nitrogen prompts biomass allocation aboveground (Poorter et al. 2012) rather than belowground as we observed. In greenhouse and field studies, Klionsky et al. (2011) recorded reduced growth and germination in native perennials in greenhouse soils amended with *R. cathartica* leaves and field soils once inhabited by *R. cathartica.* Seltzner and Eddy (2003) found the greatest inhibitory effect of *R. cathartica* on crop plants from the drupe exudates with less effect by leaves and no effect from roots. We found that root amendments generally caused the largest inhibitory effects, even with half the biomass (5 g) of the largest leaf amendment (10 g).

Given that most plants die during recruitment (germination and emergence), plant community composition is highly dependent on recruitment (Blaney and Kotanen 2001; Fenner and Kitajima 1999; Moles and Westoby 2004; Warren II and Bradford 2011), and allelopathy appears most inhibitory against competitor seedlings (Izhaki 2002; Orr et al. 2005; Pisula and Meiners 2010). We found species-specific *R. cathartica* impacts, as have several other researchers in multi-plant allelopathy studies (Cipollini and Bohrer 2016; Izhaki 2002; Klionsky et al. 2011; Small et al. 2010). Our lone non-native species, *M. vimineum* (an invasive annual) did not germinate well, possibly due to an unknown issue with long-term seed storage. When it did germinate, it only did so in the control and lowest-level *R. cathartica* treatments. *Populus deltoides* (a fast-growing canopy tree) germinated much better than *M. vimineum*, but it also only germinated in the control and lowest-dose treatments. *Liatris cylindracea* and *S. oolentangiense* (perennial herbs) recruitment generally decreased with increased leaf amendments. *Pinus strobus* (a gymnosperm canopy tree) appeared little impacted by *R. cathartica* leaf treatments and, unlike the other species, none of which germinated in the root treatment, it appeared to thrive with macerated *R. cathartica* root material. Interestingly, *P. strobus* seeds are much larger (~15–17 g) than the other plant species used here (~0.5–3 g), which may confer some sort of enhanced protection or resistance to the *R. cathartica* effects.

These results suggest that multi-species and multi-type plant studies are crucial in -determining community-level allelopathic impacts. Our mesocosm experiment suggested allelopathic effects from macerated *R. cathartica* tissues, but these results must be considered potential effects as our mode of delivery was a rapid-pulse soil amendment, which may be realistic (Heneghan et al. 2002; Schuh and Larsen 2015), but this mechanism needs to be tested in an ecologically realistic setting. Moreover, the community-level impacts may be direct allelopathy mechanisms or the indirect effects of *R. cathartica* resistance gave specific species, such as *P. strobus*, competitive advantages against the other species.

The putative key allelochemical in the genus *Rhamnus* is emodin, which has been found in all parts of the plant except roots, though it has been found in the rhizomes and roots of other plants (Izhaki 2002). Emodin, and potentially other secondary metabolites in *R. cathartica*, may be Eurasian allelochemicals against which North American organisms have not co-evolved defenses (Izhaki 2002). As such, invasive non-native plant species may bring novel weapons against which native species have little or no resistance, including novel allelochemicals (Callaway et al. 2008; Callaway and Ridenour 2004; Thorpe et al. 2009). Indeed, Thorpe et al. (2009) demonstrated that *Centaurea maculosa* (a Eurasian forb) is allelopathic in its invaded but not home range. *Rhamnus cathartica*'s novel allelochemicals also may provide indirect competitive advantage by deterring local phytophagous herbivores (Izhaki 2002; Ridenour and Callaway 2011). For example, Lepidopterans at the Tifft Nature Preserve feed extensively on native woody species but avoid *R. cathartica* (Grunzweig et al. 2015). Moreover, white-tailed deer avoid browsing *R. cathartica* at Tifft and as a result pose a visible burden on native woody seedling and saplings (*pers. obs.*).

The impacts of non-native invasive species such as *R. cathartica* likely are scale-dependent (Knight and Reich 2005; Powell et al. 2013). At larger scales, *R. cathartica* establishment seems driven by long-distance seed dispersal by birds and facilitated by habitat disturbance. Whereas *R. cathartica* can invade forest interiors, it appears to establish most successfully at forest edges or with canopy disturbance (Harrington et al. 1989; Knight et al. 2007), particularly in urban forests (Schneider and Miller 2014; Zipperer 2002). Indeed, intact, native forests appear to resist *R. cathartica* invasion (McCay and McCay 2009; Whitfield et al. 2014). However, once established, *R. cathartica* allelochemicals may protect seedlings from herbivores and augment herbaceous-layer competition against other plants. Eventually, these advantages may promote dense local populations. Hence, *R. cathartica* 's allelochemical abilities may not help it colonize new habitats as much as help the plant hold its ground after invasion.

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