A multi-assay comparison of seed germination inhibition by Lonicera maackii and co-occurring native shrubs

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A B S T R A C T
Recent work suggests that germination inhibition via allelopathy may be an important component of some species’ invasion ecology. We conducted four germination assays to test the inhibitory potential of Amur honeysuckle (Lonicera maackii), a problematic invasive shrub. The subject species in the first assay, Festuca arundinacea, exhibited a significant delay in germination when treated with extract from ground honeysuckle foliage. In the second assay, two concentrations of L. maackii extract were created by soaking foliage. F. arundinacea germination was not significantly influenced by the treatments while germination in Impatiens wallerana was substantially decreased. The third assay compared the impact of foliar extract from honeysuckle, with the native shrubs Lindera benzoin and Asimina triloba using F. arundinacea, I. wallerana, Coreopsis lanceolata, and Poo pratensis as subject species. In this assay, I. wallerana was strongly inhibited by L. maackii foliage; however, none of the other species were significantly influenced by the treatments. In the fourth assay, fruit extracts from L. maackii and L. benzoin were applied to the same four subject species. L. maackii fruit extract had an inhibitory influence on seed germination of all subject species, and inhibition from L. benzoin was also noted. Across all assays, there was a mixed reaction to extract from L. maackii and co-occurring native species that was species-specific and dependent upon the extract source. Our findings provide support for the idea that L. maackii has allelopathic activity, but further work is needed to (i) understand how broad the impact may be across the wide variety of species that are found in its invasion range and (ii) substantiate that the allelopathic effect has relevance in field environments.

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1. Introduction

Non-native invasive species often have negative consequences for native ecosystems and efforts to prevent their spread are costly (Ehrenfeld, 2003; Evans et al., 2001; Lovett et al., 2006; Pimental et al., 2000). Invasive species move aggressively into natural areas, reducing the richness and diversity of plant communities, and altering ecosystem function (Ehrenfeld, 2003; Hartman and McCarthy, 2007; Mack et al., 2000; Miller and Gorchov, 2004). Although much is known about how invasive species impact native plant communities (Collier et al., 2002; Gorchov and Trisel, 2003), less is known about the mechanisms by which invasive species establish and maintain site dominance (Meekins and McCarthy, 2001). Some promising recent work has suggested that belowground processes are important during plant invasion, and may be key to understanding how invaders proliferate in native ecosystems (Hierro and Callaway, 2003). Belowground effects of exotic species have included chemical interference (allelopathy), wherein native species’ growth and reproduction are inhibited by secondary chemicals exuded by the exotic species (Hierro and Callaway, 2003; Roberts and Anderson, 2001; Skulman et al., 2004). Compelling evidence of allelopathic effects of non-native invasive plants has come from a variety of species and regions (Callaway and Ridenour, 2004; Hierro and Callaway, 2003; Prati and Bossdorf, 2004; Skulman et al., 2004).

The deciduous shrub Amur honeysuckle (Lonicera maackii) is a non-native, invasive plant that has proliferated rapidly in east-central North America in the past 30 years (Hutchinson and Vankat, 1997; Luken and Thieret, 1996; Miller and Gorchov, 2004). It was introduced to North America from its native Asia for use as an ornamental, for wildlife cover, and to control soil erosion (Luken and Thieret, 1996). Like other plant invaders, L. maackii is encroaching into natural areas, usurping habitat space at the expense of native species (Collier et al., 2002; Hutchinson and Vankat, 1998; Miller and Gorchov, 2004). Once established, L. maackii reduces the growth and fecundity of native species (Gould and Gorchov, 2000; Gorchov and Trisel, 2003; Hartman

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and McCarthy, 2004, 2007). Although the negative influence of this species on native plant communities is well established (e.g., Collier et al., 2002; Gorchov and Trisel, 2003; Luken et al., 1997), the mechanism(s) of this influence are not well understood.

*L. maackii* negatively influences native plant communities in a variety of ways. It has a dense growth form, sprouts prolifically (Luken et al., 1995, 1997), and has a longer leaf phenology than most deciduous shrubs in the habitats it invades (McEwan et al., 2009a). Therefore, light occlusion is almost certainly an important factor limiting native species in areas where *L. maackii* occurs. Preliminary evidence also suggests that *L. maackii* seedling dominance may be facilitated by allelopathy. Skulman et al. (2004) provide compelling evidence of allelopathic activity in *Lonicer a japonica* Thunb, a congener of *L. maackii* that is also a troublesome invasive species in North America. Dorning and Cipollini (2006) demonstrated that *L. maackii* inhibits seed germination in both native and non-native forbs, without autotoxic effects. Cipollini et al. (2008b) also demonstrated that *L. maackii* extract caused a reduction in *Arabidopsis thaliana* (L.) Heynh reproductive output across a range of nutrient conditions. McEwan et al. (2009b) found that *L. maackii* leaf material was toxic to *Lymantria dispar* L., an insect herbivore with a broad host range. These studies strongly suggest that allelopathic activity could be a contributor to the suite of characteristics that enable invasion by *L. maackii*.

We conducted a series of experiments to further our understanding of the allelopathic potential of *L. maackii*. We hypothesized that (H1) *L. maackii* extract inhibits seed germination, and tested this hypothesis in a series of assays using four different subject species. One of the key aspects of allelopathy as a novel weapon associated with invasion success (Callaway and Ridenour, 2004) is the absence of this capacity in native species. In order to assess whether allelopathy represents a novel advantage for *L. maackii* that is absent from native shrubs we included native shrubs in our assays and tested the hypothesis (H2) that exudates from native shrubs found in the same habitats as *L. maackii* do not suppress seed germination.

2. Materials and Methods

2.1. Assay #1: influence of leaf extract from *L. maackii* and native ericaceous shrubs on grass seed germination.

The influence of *L. maackii* foliage on germination of *F. arundinacea* Schreb (Fayette Seed, Lexington, KY) was assessed. *Festuca arundinacea* is a grass species that is a common dominant of agricultural fields in areas where *L. maackii* is problematic, and their ecological interactions have important implications for old-field succession in the region. The influence of *L. maackii* on *F. arundinacea* germination was compared to that of two native ericaceous shrubs, *Rhododendron maximum* L. and *Kalmia latifolia* L. In this assay we also included the exotic congener, *L. japonica* as a treatment species. In November 2003, 20 g of leaf material was collected from each species in forests of eastern Kentucky, USA. A blender was used to macerate fresh leaf material in 200 ml of distilled water creating a 10:1 concentration (200 ml of solution; 20 g of fresh leaves). This concentration is similar to that used in other studies of allelopathy (e.g., Dorning and Cipollini, 2006; Roberts and Anderson, 2001). The solution was filtered through cheesecloth to remove leaf particles. Seeds of *F. arundinacea* (n=25) were placed on two sheets of Whatman #1 filter paper, in a 100 × 20 mm Petri dish (n=3, per treatment), treated with 10 ml of either plant material solution or distilled water, and sealed with Parafilm. Dishes were stored at 20 °C with a 12/12 h day–night light cycle. Germination was recorded every 24 h until germination had ceased for at least two consecutive days. At the close of the experiment root and shoot length of the seedlings were measured.

2.2. Assay #2: influence of *L. maackii* foliar extract concentration on grass and forb germination.

In the second assay we tested the germination response of a grass and a forb to two concentrations of *L. maackii* foliar extract. In addition to *F. arundinacea*, an *Impatiens wallerana* hybrid (“dwarf white baby,” Ferry Morse Seeds, Fulton KY) was added to the experiment. Adding *I. wallerana* was of ecological and experimental interest because (i) it added a forb for contrast with the response of the grass and (ii) *Impatiens* is a genus thought to be susceptible to *L. maackii* allelopathy (Dorning and Cipollini, 2006). In order to address the potential influence of distilled water, we used a simulated precipitation solution in the rest of the assays. The precipitation mimic was generated by adding chemical nutrients to distilled water until pH conductivity, alkalinity, and concentrations of NO3−, NH4+, Ca2+, Mg2+, K+, Na+, total organic carbon (TOC), Cl, and SO4= matched mean values from rain water collected in an unrelated, long-term precipitation monitoring project at Robinson Forest, in southeastern Kentucky. Leaves were collected in November of 2006 and soaked in the precipitation mimic for 24 h, at a 10:1 concentration (100 ml of solution, 10 g of fresh leaves). Seeds (n=25) of *F. arundinacea* and *I. wallerana* were placed on two sheets of Whatman #1 filter paper in a 100 × 20 mm Petri dish (n=3). Dishes were treated with either full concentration (10:1), a 50% concentration (200 ml of solution, 10 g of fresh leaves), or the simulated precipitation (i.e., control). Dishes were sealed and stored at 23 °C with a 15/9 h day/night light cycle. Germination was recorded every 24 h until germination had ceased for at least two consecutive days. At the close of the experiment root and shoot length of the seedlings were measured.

2.3. Assay #3: comparison of *L. maackii* and native shrub foliar extracts on grass and forb germination.

The third assay assessed the allelopathic influence of *L. maackii* foliar extracts compared to that of *Lindera benzoin* (L.) Blume and *Asimina triloba* (L.) Dunal, two native shrubs that have a similar growth form, and are found in the same habitats, as *L. maackii*. In addition to *F. arundinacea* and *I. wallerana*, we added *Poa pratensis* L. (Fayette Seed, Lexington, KY) and *Coreopsis lanceolata* L. (Livingston Seed Company, Columbus, OH). *P. pratensis* co-occurs with *F. arundinacea* in old-fields where *L. maackii* is a problematic invader and is also found in forest understories where it may be susceptible to *L. maackii* influence. It also provided another grass species to contrast with the response of *F. arundinacea*. *C. lanceolata* occurs in the range of *Lonicer a* invasion and provides contrast with *I. wallerana* because *Impatiens* is a genus thought to be susceptible to allelopathy, whereas the influence on *Coreopsis* is unknown. Treatment solutions were created by soaking fresh leaves (collected in November of 2006) of the three test species in the precipitation mimic for 24 h, at a 10:1 ratio (100 ml of solution, 10 g of fresh leaves). Seeds (n=20) of the subject species were placed on two sheets of Whatman #1 filter paper in a 100 × 20 mm Petri dish (n=3 control; n=36 treatments), moistened with 8 ml of solution, sealed, and grown at 25/15 °C, 15/9 h day/night. Germination was recorded every 24 h until germination had ceased for at least two consecutive days. At the close of the experiment root and shoot length of the seedlings were measured.
2.4. Assay #4: influence of L. maackii and L. benzoin fruit extracts on grass and forb germination.

In the fourth assay we evaluated the allelopathic influence of L. maackii and L. benzoin fruit on two grasses, F. arundinacea and P. pratensis, and two forbs, I. wallerana and C. lanceolata, using the methods and replication described in assay #3. Fruits were collected in November of 2006 and treatment solutions were created by macerating fruits in a blender containing a 10:1 concentration (100 ml of solution, 10 g of berries). Seeds were placed upon two sheets of Whatman #1 filter paper in a 100 ml of solution, 10 g of berries). Seeds (n=20) of the subject species were placed upon two sheets of Whatman #1 filter paper in a 100 x 20 mm Petri dish (n=3 control; n=36 treatments), moistened with 8 ml of solution, sealed, and grown at 25/15 C, 15/9 h day/night. Germination was recorded every 24 h until germination had ceased for at least two consecutive days. At the close of the experiment root and shoot length of the seedlings were measured.

2.5. Statistical analysis

Data were screened for normality using the D’Agostino omnibus test (D’Agostino et al. 1990). The mean number of seeds germinated through time was compared among treatments using repeated measures analysis of variance (RMANOVA). For these analyses, germination was the response variable, leaf extract treatment was the between-subjects factor and time (day) was the within-subjects factor. Final germination was compared among treatments using analysis of variance (ANOVA) or the Kruskal–Wallis Rank ANOVA, depending on normality. Where significant model differences were identified by the ANOVA, post-hoc multiple comparisons were used to determine differences among treatments; the Tukey–Kramer multiple comparison test was used for normally distributed data and the Kruskal–Wallis multiple comparison Z test was used otherwise. All statistical procedures were conducted using NCSS (Hintze, 2001).

3. Results

3.1. Assay #1: influence of leaf extract from L. maackii and native ericaceous shrubs on grass seed germination.

Foliar extracts from L. maackii significantly delayed germination (%) of F. arundinacea seeds compared to native ericaceous shrubs and the control (Fig. 1). The treatments had a highly significant (RMANOVA: F_{4,10}=21.1, \( P<0.001 \)) influence on seed germination. Germination of the control was nearly at its maximum by day 5; in contrast, fescue seeds treated with L. maackii leaf extract began germination on day five and did not reach their maximum until day nine (Fig. 1). Germination of seeds treated with the native shrubs K. latifolia and R. maximum was intermediate between invasive treatments and the control for virtually the entire assay (Fig. 1). At the end of the assay, the treatments were statistically indistinguishable (ANOVA: \( F_{4,10}=1.19, P=0.37 \)), meaning that the (final) total germination was not reduced by any of the treatments (relative to the control). Extract from the treatment species created statistical differences in final F. arundinacea shoot length (\( F_{4,10}=6.7; P=0.007 \)). Seeds treated with extract from L. benzoin produced shorter shoots than the control (Fig. 2). No other treatment differed from the control in final shoot length (Fig. 2).

3.2. Assay #2: influence of L. maackii leaf extract concentration on grass and forb germination.

Concentrated L. maackii extract substantially reduced total germination in I. wallerana but there was only a slight and insignificant delay in the germination of F. arundinacea (Fig. 3). Over the course of the experiment the treatments created a significant effect in I. wallerana germination (RMANOVA: \( F_{4,6}=12.6; P=0.007 \)), with germination in the control being the highest, the 1/2 concentration intermediate, and the full concentration the lowest (Fig. 3). Significant differences were not detected among treatments in final germination (ANOVA: \( F_{4,6}=2.9; P=0.13 \)). I. wallerana roots were significantly shorter in dishes treated with the fully concentrated L. maackii extract (Table 1) although the final size of its shoots was indistinguishable among treatments.

A delay in F. arundinacea germination was seemingly apparent on day 4 (Fig. 3), although the seeds were not significantly influenced by the treatments considering the entire time course (RMANOVA: \( F_{4,6}=0.54; P=0.6 \). Final germination of F. arundinacea seeds was not different among the treatments (ANOVA: \( F_{4,6}=0.27; P=0.9 \)).

![Figure 1](https://example.com/figure1.png)

*Fig. 1.* Germination of F. arundinacea seeds treated with extracts from leaves of four plant species and de-ionized water. Each point is the daily mean (± SE).
Fig. 2. Final shoot length of *F. arundinacea* seedlings treated with extracts from four plant species and a de-ionized water control. Each histogram bar represents the mean (± SE), and statistical differences (*P* < 0.05) are indicated by letters above the bars.

Fig. 3. Germination of *I. wallerana* and *F. arundinacea* seeds treated with two concentrations of *L. maackii* extract and a precipitation mimic control solution. Each point is the daily mean (± SE).
0.77; Fig. 3). *F. arundinacea* seeds did exhibit differences in growth due to *L. maackii* extract; those treated with the full concentration produced longer roots and shoots than either the 1/2 concentration or the control (Table 1). Confusingly, *F. arundinacea* seedlings treated with 1/2 concentration had shoots that were shorter than either the control or full concentration treatment (Table 1).

### 3.3. Assay #3: comparison of *L. maackii* and native shrub leaf extracts on grass and forb germination.

Leaf extracts from *L. maackii* and native shrubs similarly influenced seed germination (Fig. 4). Leaf extract from *L. maackii* created an apparent delay in the germination of *F. arundinacea* on day 4 that was also evident for extracts of *A. triloba* and *L. benzoin*

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**Table 1**

Mean (± SE) final seedling root and shoot length (mm) of *F. arundinacea* and *I. wallerana* seedling treated with leaf extract from *L. maackii* at two concentrations and a rain water mimic control.

<table>
<thead>
<tr>
<th>Treatments</th>
<th><em>I. wallerana</em></th>
<th><em>F. arundinacea</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Root</td>
<td>Shoot</td>
</tr>
<tr>
<td>Full concentration</td>
<td>05.1 ± 0.2a</td>
<td>5.7 ± 0.3</td>
</tr>
<tr>
<td>½ concentration</td>
<td>11.5 ± 1.8b</td>
<td>7.1 ± 1.5</td>
</tr>
<tr>
<td>Control</td>
<td>21.9 ± 7.8b</td>
<td>6.2 ± 1.5</td>
</tr>
</tbody>
</table>

|                   | *H* = 6.49     | *F* = 0.33       | *F* = 47.0      | *F* = 42.5       |
|                   | *P* = 0.039    | *P* = 0.72       | *P* < 0.001     | *P* < 0.001      |

Statistical differences (*P* < 0.05) among treatments (within columns) indicated by bold letters, and statistical values are posted in the bottom of columns. *H* values are reported for Kruskal–Wallis rank ANOVA, *F* values for parametric ANOVA.

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**Fig. 4.** Germination of four subject species when treated with leaf extract from three treatment species and a precipitation mimic control solution. Each point is the daily mean (± SE).
One puzzling aspect of plant invasion is that the species in question are often infrequent and innocuous in native habitats, but proliferate aggressively and form near-monoculture stands in their invaded habitats these plants contain secondary compounds that facilitate acquisition of habitat space (Callaway and Ridenour, 2004; Hierro and Callaway, 2003; Prati and Bossdorf, 2004). An allelopathic component in the invasion ecology of diffuse knapweed has been demonstrated (Centaurea diffusa Lam.; Callaway and Aschehoug, 2000), and preliminary work suggests that allelopathy may play a role in garlic mustard (Prati and Bossdorf, 2004) and Japanese honeysuckle (Skulman et al., 2004) invasions. Overall, a growing body of work supports the idea that allelopathy is a contributing factor in some plant invasions.

Table 2
Mean (± SE) final seedling root and shoot length (mm) from four subject species treated with leaf extract from three treatment species and a rain water mimic control.

<table>
<thead>
<tr>
<th>Treatments</th>
<th>F. arundinacea</th>
<th>P. pratensis</th>
<th>L. wallerana</th>
<th>C. lanceolata</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Root</td>
<td>Shoot</td>
<td>Root</td>
<td>Shoot</td>
</tr>
<tr>
<td>L. maackii</td>
<td>81.5 ± 9.4</td>
<td>57.1 ± 5.2</td>
<td>35.6 ± 3.9a</td>
<td>23.6 ± 0.6</td>
</tr>
<tr>
<td>L. benzoin</td>
<td>76.9 ± 3.4</td>
<td>57.6 ± 2.6</td>
<td>40.5 ± 2.8a</td>
<td>23.6 ± 2.2</td>
</tr>
<tr>
<td>A. triboa</td>
<td>59.4 ± 3.7</td>
<td>51.3 ± 1.6</td>
<td>11.9 ± 1.4b</td>
<td>19.1 ± 1.8</td>
</tr>
<tr>
<td>Control</td>
<td>53.4 ± 2.1</td>
<td>48.1 ± 4.3</td>
<td>18.0 ± 2.9b</td>
<td>20.6 ± 1.6</td>
</tr>
</tbody>
</table>

H_0=15.13 H_1=6.28 H_2=7.31 H_3=3.16 H_4=5.03 H_5=6.00 H_6=4.76

P=0.06 P=0.10 P=0.002 P=0.063 P=0.34 P=0.16 P=0.11 P=0.19

Statistical differences (P < 0.05) among treatments (within columns) indicated by bold letters, and statistical values are posted in the bottom of columns. All tests reported here were from Kruskal–Wallis rank ANOVAs, followed by multiple comparison Z tests.

4. Discussion

Germination of L. wallerana seeds was significantly influenced by the fruit extracts (RMANOVA: F_{2,12}=16.09; P < 0.001). Throughout the experiment, the control exhibited the (apparently) highest germination (Fig. 5C, D). At the end of the experiment, final germination was significantly influenced by the treatments (ANOVA: F_{2,12}=12.86; P < 0.001) with the control statistically separated from both treatments (Tukey–Kramer multiple comparison test, P < 0.05), which were indistinguishable from one another. C. lanceolata seed germination was significantly influenced by the treatments over the time course of the experiment (RMANOVA: F_{2,12}=5.16; P = 0.02), and seeds treated with fruit solution from L. maackii and L. benzoin exhibited a similar delay in germination (Fig. 5D). By the end of the experiment, though, there were no treatment differences (ANOVA: F_{2,12}=12.86; P = 0.16).

Seedling response to fruit extracts differed (Table 3). The root length of F. arundinacea treated with L. benzoin fruit extract was significantly greater than either the L. maackii berry treatment or the control, which were indistinguishable (Table 3). Shoot length of F. arundinacea did not differ among treatments. P. pratensis root length and shoot length were significantly shorter for seedlings treated with L. maackii berry extract (Table 3). Final root length of L. wallerana seedlings treated with L. maackii berry extract were significantly shorter either the L. benzoin treatment or the control. Shoot length of L. wallerana, and root and shoot length of C. lanceolata, did not differ among treatments (Table 3).


Extract from the fruit of L. maackii influenced germination of both grasses and forbs, while L. benzoin fruit extract affected only forbs (Fig. 5). In F. arundinacea, there was a highly significant effect of the treatments on germination (RMANOVA: F_{2,12}=30.9; P < 0.001). Through most of the time course, germination of seeds treated with L. maackii was clearly separated from the other two treatments (Fig. 5A). There was a significant effect of the treatments on final germination (ANOVA: F_{2,12}=6.14; P = 0.01) where the seeds treated with L. maackii were indistinguishable from the control, and germination for both were statistically lower than seeds treated with L. benzoin fruit pulp (Tukey–Kramer multiple comparison test, P < 0.05). P. pratensis seeds were markedly influenced by the treatments (RMANOVA: F_{2,12}=25.2; P < 0.001) and exhibited substantially lower germination when treated with L. maackii fruit extract than when treated with L. benzoin or the control (Fig. 5B). Final germination reflected this general pattern—there was a significant effect of the treatments (ANOVA: F_{2,12}=17.66; P < 0.001), and the L. maackii treatment was significantly separated from the other two treatments (Tukey–Kramer multiple comparison test, P < 0.05).
competitive advantage in the habitats it invades. The fecundity of native herbaceous species is reduced by the presence of *L. maackii* (Gould and Gorchov, 2000), and native tree seedling survival is enhanced by its removal (Hartman and McCarthy, 2004). Gorchov and Trisel (2003) provide evidence that belowground factors are important in the invasion of *L. maackii* and demonstrate its capacity to reduce the growth of native tree seedlings such as *Acer saccharum*. Dorning and Cipollini (2006) suggest that *L. maackii’s* competitive advantage, and capacity for suppression, could be linked to allelopathy and demonstrate inhibitory effects of foliar extract on seed germination of four herbaceous species. Cipollini et al. (2008a) showed that *L. maackii* extract added to soil in a growth chamber reduced both the number and size of *A. thaliana* siliques across a range of soil nutrient conditions, and Cipollini et al.

**Table 3**

Mean (± SE) final seedling root and shoot length from four subject species treated with fruit extract from two treatment species and a rain water mimic control.

<table>
<thead>
<tr>
<th>Treatments</th>
<th><em>F. arundinacea</em></th>
<th><em>P. pratensis</em></th>
<th><em>L. wallerana</em></th>
<th><em>C. lanceolata</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Roots</td>
<td>Shoots</td>
<td>Roots</td>
<td>Shoots</td>
</tr>
<tr>
<td><em>L. maackii</em></td>
<td>32.7 ± 03.0a</td>
<td>56.2 ± 02.0a</td>
<td>12.8 ± 0.8a</td>
<td>0.8a</td>
</tr>
<tr>
<td><em>L. benzoin</em></td>
<td>65.3 ± 04.2b</td>
<td>57.9 ± 01.8a</td>
<td>21.3 ± 1.7b</td>
<td>3b</td>
</tr>
<tr>
<td>Control</td>
<td>40.3 ± 13.0a</td>
<td>41.5 ± 11.6a</td>
<td>22.5 ± 2.0b</td>
<td>6b</td>
</tr>
<tr>
<td><em>F</em>&lt;sub&gt;2,12&lt;/sub&gt;=11.2</td>
<td><em>H</em>&lt;sub&gt;2&lt;/sub&gt;=4.9</td>
<td><em>F</em>&lt;sub&gt;2,12&lt;/sub&gt;=20.8</td>
<td><em>F</em>&lt;sub&gt;2,12&lt;/sub&gt;=13.4</td>
<td><em>F</em>&lt;sub&gt;2,12&lt;/sub&gt;=8.9</td>
</tr>
<tr>
<td><em>P</em>=0.002</td>
<td><em>P</em>=0.09</td>
<td><em>P</em>=0.001</td>
<td><em>P</em>=0.004</td>
<td><em>P</em>=0.023</td>
</tr>
</tbody>
</table>

Statistical differences (*P* < 0.05) among treatments (within columns) are indicated by bold letters. *H* values are reported for Kruskal–Wallis rank ANOVA, *F* values for parametric ANOVA.

**Fig. 5.** Germination of three subject species when treated with fruit extract from two treatment species and a precipitation mimic control solution. Each point is the daily mean (± SE).
invasive species may dominate habitat space in communities they invade. Identifying these attributes, and clarifying the relative importance of each, will further our ecological understanding of these problematic species and facilitate the management of plant invasions.

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