Avian seed dispersal of an invasive shrub

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Received 30 November 2004; accepted in revised form 10 March 2005

Key words: American robin, cedar waxwing, exotic plant, Lonicera maackii, Ohio, seed germination, seed shadow, seed viability

Abstract

The incorporation of an animal-dispersed exotic plant species into the diet of native frugivores can be an important step to that species becoming invasive. We investigated bird dispersal of *Lonicera maackii*, an Asian shrub invasive in eastern North America. We (i) determined which species of birds disperse viable *L. maackii* seeds, (ii) tested the effect of gut passage on *L. maackii* seeds, and (iii) projected the seed shadow based on habitat use by a major disperser. We found that four native and one exotic bird species dispersed viable *L. maackii* seeds. Gut passage through American robins did not inhibit germination, but gut passage through cedar waxwings did. American robins moved mostly along woodlot edges and fencerows, leading us to project that most viable seeds would be defecated in such habitats, which are very suitable for *L. maackii*. We conclude that *L. maackii* has been successfully incorporated into the diets of native and exotic birds and that American robins preferentially disperse seeds to suitable habitat.

Abbreviations: AMRO – American robin; CEWA – Cedar waxwing

Introduction

The ability of exotic plants to incorporate native animal species in mutualistic interactions such as pollination or seed dispersal is often a key factor in their becoming invasive (Richardson et al. 2000). Many generalist pollinators and biotic dispersal agents have been documented to incorporate these new resources into their diets (Richardson et al. 2000; Reichard et al. 2001 for review). Seed dispersal has been described as a 'diffuse mutualism' due to the fact that most, if not all, frugivores consume fruits of many different species of plants (Wheelwright and Orians 1982; Jordano 1995). This has resulted in little coupling between the characteristics of fruits and their vertebrate dispersers (Jordano 1995). That fruit-bearing plants live longer than frugivores (Herrera 1985) has led to the hypothesis that frugivores more easily adjust their diets to incorporate new fruits easier than plants can adapt to new dispersers (Howe and Westley 1997). Examples of bird species in North America that have incorporated fruits of invasive plants into their diet and presumably disperse their seeds include European starlings (Sturnus vulgaris) (La Rue 1994), northern mockingbirds (Minus polyglottos) (Stiles 1982), and cedar waxwings (CEWAs) (Bombycilla cedrorum) (Witmer 1996). Renne et al. (2002) found that many species of native and exotic birds incorporated fruit of the invasive Chinese tallow tree (Sapium sebiferum) in their diets in South Carolina.

The quality of seed dispersal that invasive plants gain from native or exotic animals is a function of both gut treatment and the spatial distribution of dispersed seeds (seed shadow). For seeds of native plants, passage through bird guts may increase, decrease, or not affect germination, depending on the species of bird and plant (Clergeau 1992; Murray et al. 1994; Crossland and Vander Kloet 1996: Traveset 1998; Cypher and Cypher 1999; Yagihashi et al. 1999; Traveset et al. 2001). However, little is known of how seeds of invasive plants are affected by gut passage through these novel seed dispersers. In one of the few published studies, Renne et al. (2001) found that seeds of Chinese tallow tree had higher germination after gut passage through native birds.

Seed shadows are shaped by gut passage time and animal movement patterns, but only a few studies have projected seed shadows based on such data (Murray 1988; Izhaki et al. 1991; Sun et al. 1997; Wescott and Graham 2000; Vellend et al. 2003). Murray (1988) determined that the major avian disperser of shade intolerant shrubs in Monteverde, Costa Rica, did not preferentially disperse seeds to tree-fall gaps. White-tailed deer (*Odocoileus virginanus*) have been projected to disperse native and exotic understory species over long distances (Vellend et al. 2003).

Movement patterns of dispersers are not fixed, but are dependent on landscape structure. Birds, for example, often follow landscape cues to fly between patches of habitat or to avoid predators. Machtans et al. (1996) found greater movements of birds through buffer strips in clearcut forests than through the clearcut areas themselves. Juvenile birds in particular used the buffers as corridors to other areas of suitable habitat. Machtans et al. (1996) also hypothesize that there is a threshold distance birds will not cross to get to other areas of habitat. Haas (1995) determined American that robins (AMROs) moved between areas of suitable habitat significantly more often when the areas were connected by corridors. She cautions, however, that these birds were capable of moving long distances without the aid of corridors. Wegner and Merriam (1979) found that birds frequently flew along fencerows to get to other suitable areas. Johnson and Adkisson (1985) determined that most blue jays dispersing seeds of beech trees flew along fencerows and hypothesized that this was a consequence of predator avoidance.

Whereas the studies described above document how landscape structure affects bird movement, they do not investigate effects on seed dispersal. An experimental study by Tewksbury et al. (2002) determined that more seeds of a bird-dispersed holly were moved between two patches connected to one another via a corridor than between unconnected patches of equal size. Few, if any, other studies directly link landscape cues to seed dispersal via animal movement.

We investigated the role of birds in the seed dispersal of the invasive shrub, Lonicera maackii (Rupr.) Herder (Caprifoliaceae). L. maackii is a popular landscape plant in eastern North America, in part because its red fruits remain on the shrub long into the winter. These fruits are consumed by many migrant and resident birds (Ingold and Craycraft 1983), but it is not known which of these disperse viable seeds. The fruits are bright red, globose, 3.5-8.5 mm in diameter (Luken and Thieret 1995), and contain an average of 4.6 seeds (DLG unpubl data). Fruits are low quality (sensu Stiles (1980)) due to their low lipid content (about 4.5-5%, Ingold and Craycraft 1983). Ingold and Craycraft (1983) observed that most L. maackii fruits remain on shrubs until periods of extreme cold or precipitation, and suggested that they were an important food source for overwintering birds.

The purpose of this project was threefold: (i) to determine which species of birds disperse viable seeds, (ii) to determine if gut passage enhances the germination of L. maackii seeds, and (iii) to determine the habitat-specific seed shadow generated by a major disperser of L. maackii seeds.

Methods

Lonicera maackii is native to northeast Asia and was introduced to the United States in 1898 as an ornamental (Luken and Thieret 1996). It has

since escaped cultivation and is invasive in 24 states east of the Mississippi River, spreading from many metropolitan areas (Trisel and Gorchov 1994). L. maackii is an upright shrub capable of germinating under a variety of light intensities and growing in many different types of habitat, including second-growth forest and old fields (Luken and Goessling 1995; Luken et al. 1997). L. maackii reduces the growth and fecundity of native annual and perennial forest herbs (Gould and Gorchov 2000; Miller and Gorchov 2004) and survival of tree seedlings (Gorchov and Trisel 2003). Additional evidence for a negative effect of L. maackii on native plants is the negative relationships between L. maackii density and density of Acer saccharum (Hutchinson and Vankat 1997; Medley 1997) and two native shrub species (Medley 1997). Collier et al. (2002) determined that species richness of native herb and tree seedlings was lower under the crowns of L. maackii.

Determination of seed dispersers

We set mist nets near fruiting *L. maackii* shrubs around Oxford, Butler County, Ohio, from November to December 2000, and at sites in Darke County, Ohio, in November–February 2001–2004 (see Bartuszevige 2004 for further details). We placed each captured bird in a cotton athletic sock for 1 h to collect a fecal sample. We released birds 1 h after capture, investigated the fecal samples for intact *L. maackii* seeds, and tested seeds for viability or germination using methods described below.

Gut retention

To estimate seed passage rates, we held four AMROs and one CEWA captive in small $(0.4 \text{ m} \times 0.4 \text{ m} \times 0.4 \text{ m})$ cages at an animal care facility at Miami University. We maintained them on an artificial diet of banana mash and soy protein (Denslow et al. 1987), fruits found in the area (primarily *Ligustrum vulgare*) and water when experiments were not in progress. During experiments, we presented each bird with a *L. maackii* branch thinned to 10 fruits and

allowed it to eat for 5 min. After that time, we removed uneaten fruits and replaced with maintenance diet. We designated the midpoint in time between when the first and last fruits were eaten as time zero. Every 5 min thereafter, we removed paper from the bottom of the cage and recovered the defecated seeds. We ended feeding trials when 30 min passed without a bird passing a *L. maackii* seed. We started feeding trials within 24 h of capture of the birds and held individual birds for ≤ 48 h.

Seed viability after gut passage

To determine the effects of gut passage on *L. maackii* seed germination, we compared seeds (1) from fecal samples collected from captured individuals used in seed passage rate trials, (2) removed from the fruit pulp by hand, and (3) in intact fruits (with pulp). We planted collected seeds in small petri dishes with sand and put into lighted environmental chambers maintained for 12 h at 25 °C and 12 h at 15 °C for 12 weeks followed by 12 h at 20 °C and 12 h at 10 °C for 2 weeks, the laboratory conditions found to result in the highest germination (Hidayati et al. 2000).

We tested seeds that failed to germinate for viability using a tetrazolium test (Grabe 1970). We placed seeds between sheets of filter paper and wetted with tap water. Approximately 24 h later, we drained the water from the petri dish and put a small puncture hole into each seed coat at the opposite end of the seed from the radicle. We added a 0.01% solution of 2,3,5triphenyltetrazolium to the petri dish to cover all the seeds. Approximately 24 h later, we cut seeds open using a razor blade and examined radicles under a dissecting microscope. Tetrazolium reacts with respiring radicles to produce a pink stain (Grabe 1970). A white radicle indicated that the seed was not viable.

We compared the frequency of seeds that germinated between pairs of treatments using G^2 log-likelihood contingency tests, with α corrected for multiple comparisons using the Bonferroni correction (Sokal and Rohlf 1997). We performed six possible comparisons for a corrected α value of 0.0083.



Figure 1. Number of intact seeds passed by captive American robins in 5 min intervals following fruit consumption. Viable seeds are indicated by filled portion of the bar, inviable seeds by the open portion. The proportion of the viable seeds passed in each interval was used as the seed passage vector, which was multiplied by the habitat matrix to project the seed shadow.

Seed shadow

We chose to project the seed shadow generated by AMROs based on this species' passage of viable seeds and abundance in the study area. We mist-netted robins at fruiting L. maackii shrubs and banded them with a U.S. Fish and Wildlife aluminum band, a unique combination of plastic color bands, and a radio transmitter with a unique frequency (Holohil Systems, Ltd. mass = 0.9 g, frequency = 151.000-151.999 Hertz). We attached the radio transmitter to the bird using a harness that fits over the legs of the bird and rests on the synsacrum ('tail bone') (similar to Rappole and Tipton 1991). We released the birds at their point of capture.

Approximately 24 h after release, we attempted to relocate each bird by searching for the transmitter frequency with a receiver. If a bird was relocated, we tracked it for 2 h after it had been observed consuming *L. maackii* fruits. We recorded all movements of the birds and the habitats in which they were located on a digital voice recorder. We recognized six different habitat types in our study area: field, interior woodlot, edge woodlot, stream, corridor (fencerow connecting two woodlots), and spur (fencerow that leads out from a woodlot but does not connect to a second woodlot). We considered the edge of the woodlot to extend 5 m into the woodlot from the perimeter. Likewise, we used a 5 m buffer around streams to calculate stream habitat area. During the observation sessions, we marked each location of the bird by placing a numbered flag at the location after it had moved on to its next location. After the session was completed, we fixed the locations of the numbered flags with a GPS receiver (Garmin GPS 48).

We pooled data from all observation sessions to parameterize a probability matrix of habitat versus time that describes the probability of a bird being in a certain habitat at a certain time after feeding on L. maackii, similar to the distance versus time matrix pioneered by Murray (1988). We divided each tracking session into 5 min intervals and the amount of time the birds spent in each habitat during that time period was summed (Bartuszevige 2004). We converted these raw times to the proportion of time spent in each habitat within each 5 min time period (Bartuszevige 2004). We multiplied this matrix by a seed passage time vector (Figure 1; based on 60 viable seeds passed by AMROs in feeding trials)

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to project the proportion of viable seeds deposited in each habitat.

To determine the proportion of habitat available in the landscape, we analyzed digital ortho quarter quad photos using ArcView GIS. We created a buffer distance of 500 m around the center of the start points for all birds radio-tracked. We selected a 500 m buffer radius because it was the longest single flight distance we observed for a robin. We converted the area of each habitat to a proportion of the entire landscape. We used a goodness of fit test to determine if the time spent in different habitats by AMROs, and therefore the projected deposition of seeds to these habitats differed, from that expected based on the representation of these habitats in the landscape.

Results

Determination of seed dispersers

We caught 17 different species of birds in nets near fruiting *L. maackii* shrubs; five of these defecated viable seeds (American robin (AMRO), cedar waxwing (CEWA), European starling, hermit thrush (*Catharus guttatus*), and northern mockingbird (*Mimus polyglottus*), Table 1) and

Table 1. Bird species that voided intact Lonicera maackii seeds, number of each captured near fruiting L. maackii shrubs, total number of intact L. maackii seeds recovered from their feces, and the percentage of these seeds that were viable. Birds are listed in phylogenetic order. Dates birds were mist-netted is reported in Bartuszevige (2004).

Bird species	# birds	# seeds	% of seeds viable
Turdinae			
Catharus guttatus	3	3	100
(Hermit Thrush)			
Turdus migratorius	23	54	94
(American Robin)			
Mimidae			
Mimus polyglottos	2	4	75
(Northern Mockingbird)			
Sturnidae			
Sturnus vulgaris	7	23	100
(European Starling)			
Bombycillidae			
Bombycilla cedrorum	6	78	83
(Cedar Waxwing)			

12 did not (American tree sparrow (Spizella arborea), brown creeper (Certhia americana), Carolina chickadee (Poecile carolinensis), Carolina wren (Thryothorus ludovivianus), dark-eyed junco (Junco hyemalis), downy woodpecker (Picoides pubescens), golden-crowned kinglet (Regulus satrapa), northern cardinal (Cardinalis cardinalis), song sparrow (Melospiza melodia), tufted titmouse (Baeolophus bicolor), white-breasted nuthatch (Sitta carolinensis), and white-throated sparrow (Zonotrichia albicollis)). Seven of the latter 12 species (American tree sparrow, Carolina chickadee, dark-eyed junco, northern cardinal, song sparrow, tufted titmouse, and white-throated sparrow) had red feces indicating they were eating L. maackii fruits, but seeds were absent or represented only by empty seed coats.

Gut retention

Of seeds (n = 34) voided by the CEWA (n = 1), 47% were viable (Figure 2). Of seeds (n = 70) voided by AMROs (n = 4), 86% were viable, significantly more than for waxwings (G = 16.35, all tests df = 1, critical value = 0.0083). Of seeds removed from the fruits by hand, 76% were viable, significantly higher viability than for seeds passed by CEWAs (G = 8.67), but not different than for seeds passed by robins (G = 2.32, Figure 2). Only 44% of seeds left in intact fruits were viable, significantly less than those passed by robins (G = 20.72) or removed by hand (G = 11.81), but not different than those passed by waxwings (G = 0.09, Figure 2).

All seeds were voided by the CEWA within 30 min (range 15–30 min). AMROs voided all seeds within 70 min (range 10–70 min). For the 60 viable seeds voided by robins, the proportions voided in each 5 min interval comprise the seed passage time vector, Figure 1.

Seed shadow

We tracked two AMROs for a total of four sessions (6.5 h), each beginning after the bird was first observed consuming L. maackii fruits. These two robins spent most of their time at the edge of the woodlot and in spurs, and very little time



Figure 2. Viability of seeds passed by cedar waxwings (n = 1) and American robins (n = 4) compared to seeds removed from fruits by hands and left in intact fruits. Bars with different letters above them are significantly different (G^2 tests with Bonferroni correction for multiple comparisons). CEWA = L. maackii seeds consumed by cedar waxwing (n = 29 seeds), AMRO = L. maackii seeds consumed by American Robin (n = 70), Removed = L. maackii seeds removed from fruits by hand (n = 63), and Whole = L. maackii seeds left in intact fruits (n = 41).

in the interior of the woodlot, in corridors, and near streams, and no time in fields (data reported in Bartuszevige 2004). Multiplying the habitat \times time matrix (Bartuszevige 2004) by the seed passage time vector (Figure 1) projects a seed shadow in which



Figure 3. Habitat seed shadow projected for American robins (n = 2 birds, n = 60 seeds) generated by multiplying the habitat × time matrix (Bartuszevige 2004) by the seed passage time vector (Figure 1), compared to the proportion of habitat available in a 500 m buffer around the midpoint of the start points of the American robin radio-tracking sessions. The value above the corridor category (0.003) is the proportion of habitat as corridor, this value was too small to show up as a bar on the graph.

most viable seeds are defecated in the spurs and at the edge of the woodlot (Figure 3). Streams, corridors and the woodlot interior also had some seed input.

This predicted seed shadow contrasts with that expected based on the abundance of the habitat composition surrounding the area where robins were captured and released (G = 341.3, df = 5, P < 0.001, Figure 3). Our seed shadow suggests that more viable seeds were deposited in edges, spurs, corridors, and streams, and less in forest interior and fields, than expected.

Discussion

Of the 17 species we determined to consume *L. maackii* fruits, only five acted as seed dispersers. We found viable seeds in the feces of the main winter resident frugivores in southwest Ohio: American robins, European starlings, hermit thrushes, cedar waxwings, and northern mockingbirds. Eastern bluebird (*Sialia sialis*) is also a likely disperser of *L. maackii* seeds. We were unable to catch any birds of this frugivorous species, but did observe them eating *L. maackii* fruits. Other birds consumed *L. maackii* fruits but did not void viable seeds. These birds are primarily granivores and digested the seeds as well as the fruit.

By inspecting feces for intact *L. maackii* seeds and testing those seeds for viability/germination, we were able to determine which bird species were dispersing viable *L. maackii* seeds. Ingold and Craycraft (1983) performed their study in the early fall (mid-September through mid-November), and based on the scarcity of *L. maackii* seeds collected from the birds they caught, concluded that fruits were eaten later in the fall and into the winter when higher quality fruits were exhausted. Results from a fruit trap study show that more *L. maackii* fruits are removed later in the season (November–February) and that fruit removal is also related to temperature and precipitation events (Bartuszevige 2004).

Due to their abundance, AMROs and European starlings are important dispersers of *L. maackii* in our study area. Although we were able to capture starlings only once, we observed large flocks of the birds foraging in *L. maackii*

shrubs. In addition, inspection of fecal material after a flock of starlings had abandoned a site revealed many whole *L. maackii* seeds in the feces. Renne et al. (2002) found that European starlings were capable of dispersing viable seeds of the invasive Chinese tallow tree. Positive interactions between an invasive plant and an invasive seed disperser may lead to an invasional meltdown where facilitative interactions between non-indigenous species increase and possibly magnify a negative ecological effect (Simberloff and Von Holle 1999).

Passage through the guts of a frugivorous bird was not required for germination of L. maackii, and in the case of CEWAs, was actually detrimental. Seeds removed from fruits by hand had a higher (vs. CEWAs) or similar (vs. AMROs) germination rate to those seeds consumed by birds. Seed removal from fruits without fruit consumption is possible if mammals step on the intact fruits that have fallen to the ground or birds drop half-eaten fruits thus freeing the seeds. Seeds left in intact fruits often germinated, but less frequently, than those seeds passed through AMROs or removed by hand. Similarly, seeds in intact Prunus fruits had lower germination success than seeds ingested by native frugivorous birds or removed from the fruits by hand (Yagihashi et al. 1999). Lower germination success of seeds remaining in intact fruits may be due to several reasons including attack by fungi or bacteria (Crossland and Vander Kloet 1996; Cipollini and Levey 1997; Yagihashi et al. 1999), low light levels, or secondary metabolites (Cipollini and Levey 1997). Clergeau (1992) found that seeds from four different plant species left in intact fruits had lower germination success than seeds removed by hand and seeds ingested by birds. He also found that the effect of bird ingestion on germination was different for different species of birds and attributed this to differential abrasion of the seed coats by the birds' guts. Seeds from some species of plants require scarification for successful germination.

The negative effect of CEWA gut passage on *L. maackii* seed germination is opposite of what we would have predicted based on diet preferences. CEWAs have a more fruit-based diet than AMROs, which are more omnivorous (Witmer 1996). Because they are more frugivorous, CE-

WAs would be expected to treat seeds more gently than AMROs (McKey 1975). However, Witmer (1994) found that fecal material from CEWAs which fed exclusively on fruits is more acidic than fecal material from AMROs fed on the same diet. The higher acidity of the feces from CEWAs may inhibit the germination of L. maackii seeds. Seeds defecated by CEWAs sown with fecal material had lower germination success than those sown without fecal material (Meyer and Witmer 1998). In addition, seeds passed through CEWAs had similar germination rates as seeds passed through other fruit-eating birds, including AMROs, when cleaned of fecal material (Meyer and Witmer 1998). Though we removed seeds from feces, we did not clean them of the fecal material, which may have inhibited germination of seeds passed by waxwings.

Based on seed passage time and movements after feeding on *L. maackii*, we projected AMROs to disperse seeds of this invasive shrub primarily to edge habitats, including wooded corridors and spurs. Although only two robins were successfully radio-tracked, each bird was part of a larger foraging flock of approximately 20 birds. These loose flocks of birds were observed flying to the same or similar habitats as the radio-tagged individuals. Furthermore, others have reported that robins preferentially use woodlands and areas where trees and shrubs are mixed with short grass in the winter as they do during the breeding season (Sallabanks and James 1999).

Similarly, in an Illinois woodland, significantly more bird-dispersed seeds were dispersed to tree-fall gaps, preferable habitat for most of the species, than to understory sites (Hoppes 1988). In a tropical ecosystem, Murray (1988) found that understory birds did not preferentially disperse seeds to forest gaps, contrary to his predictions. Rather birds seemed to move between sources of abundant fruit. Movement between sources of abundant fruit could also explain the movement patterns of robins. We observed that the most abundant fruit sources were at the edges of the woodlots. Thus robins seem to be participating in a positive feedback loop of L. maackii invasion. L. maackii is often found at the edges of woodlots where individual shrubs grow to be 2-3 m tall and produce thousands of fruits (pers obs). Robins feed at these shrubs and move to other fruiting shrubs at the edges of the woodlots and presumably defecate viable seeds at these same edges. This potential nonrandom dispersal of L. maackii seeds to favorable sites by AMROs may be an example of directed dispersal (Howe and Smallwood 1982). However, dispersal of seeds beneath conspecific plants may increase mortality due to seed predation or intraspecific competition (Howe and Smallwood 1982; Wheelwright and Orians 1982), although White et al. (1992) found that seed predation on L. maackii by small mammals was unlikely to affect seed survival. Intraspecific competition between L. maackii seedlings has not been demonstrated and any negative effects of competition are likely outweighed by the greater rates of L. maackii germination and growth in high light environments such as a woodlot edge (Luken et al. 1995).

Mammals, most notably white-tailed deer (Odocoileus virginianus) may also consume L. maackii fruits and act as seed dispersal agents. Vellend (2002) surveyed deer pellets in New York and found viable seeds of L. morrowii and L. tartarica in 69 of 72 pellets collected and calculated that they can move these seeds more than 1 km. Deer consumption of L. maackii fruits may be rare as they ripen later (September) than L. morrowii and L. tatarica (July/August) and we rarely found evidence of browse. But if deers consume L. maackii fruit, and if the soft seeds survive gut passage, they are likely to be an important seed dispersal vector due to their high density in many environments (Halls 1984), ability to consume larger quantities of fruits than seed-dispersing birds (Vellend 2002), and their wide-ranging daily and migratory movement patterns (Vellend 2002; Myers et al. 2004).

Conclusions

Mutualistic interactions between native and exotic bird species and *L. maackii* are important during the invasion of this shrub into new sites. Many birds species consume *L. maackii* fruits during the winter in southwest Ohio, but only five species of birds disperse its seeds. Seed dispersal by birds, combined with the ability to germinate without gut passage, makes control of this species difficult. Established populations will likely be able to recruit more shrubs beneath their canopies, while seeds dispersed by birds can germinate in new sites. AMROs tend to move along the edges of woodlots and disperse seeds to these highly suitable habitats.

Acknowledgments

We thank Steve Beiting, Adriane Carlson, Kristy Combs, David Creager, Erin Cross, Chris Davis, Nick Drozda, Mike Gilmore, Jessica Hawk, Rikki Hrenko, Jeff Kroll, Sasha Lucas, Melissa Olenik, Maria Palmieri, Nathan Sammons, Cary Snyder, Emily Stuebing, Dawn Trexel, and Casey Tucker for assistance in the field. Mike Hughes and John Bailer provided statistical assistance. Miami University Ecology Research Center provided animal care facilities. All experiments with birds were completed with the appropriate federal, state, and institutional permits. This project was funded by U.S. Department of Agriculture National Research Initiatives Invasive and Weedy Plants Program (# CG00717), Miami University Academic Challenge, and Garden Club of Ohio.

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