A landscape perspective of the stream corridor invasion and habitat characteristics of an exotic (*Dioscorea oppositifolia*) in a pristine watershed in Illinois

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Abstract

The spatial distribution of exotics across riparian landscapes is not uniform, and research elaborating the environmental constraints and dispersal behavior that underlie these patterns of distribution is warranted. This study examined the spatial distribution, growth patterns, and habitat constraints of populations of the invasive *Dioscorea oppositifolia* in a forested stream corridor of a tributary of Drury Creek in Giant City State Park, IL. The distribution of *D. oppositifolia* was determined at the watershed scale mainly by floodplain structure and connectivity. Populations of *D. oppositifolia* were confined to the floodplain, with overbank flooding from the stream. *Dioscorea oppositifolia* probably originates in disturbed areas upstream of natural corridors, and subsequently, the species disperses downstream into pristine canyons or ravines via bulbils dispersing in the water. In Giant City State Park, populations of *D. oppositifolia* were distributed on the floodplain across broad gradients of soil texture, light, slope, and potential radiation. The study also examined the longevity of bulbils in various micro-environments to illuminate strategies for the management of the species in invaded watersheds. After 1 year, the highest percentages of bulbils were viable under leaves, and much lower percentages were viable over leaves, in soil, and in the creek (76.0 ± 6.8, 21.2 ± 9.6, 21.6 ± 3.6, and $5.2 \pm 5.2\%$), respectively. This study suggests that management procedures that reduce leaf litter on the forest floor (e.g., prescribed burning) could reduce the number of bulbils of *D. oppositifolia* stored in the watershed.

Introduction

The invasion dynamics of exotic species in riparian ecosystems could be dependent to a large extent on the physical characteristics of the watershed (Planty-Tabacchi et al. 1996), particularly the interconnectivity between invaded upstream sites and uninvaded downstream sites (Gregory et al. 1991; Parendes & Jones 2000). Thus, flood-plains may be more prone to invasion by exotics than surrounding landscapes because of increased opportunities for propagule dispersal in water, and the physical disturbances created by water movement and flooding on the floodplain. Ultimately, the spatial distribution of invasive species in riparian zones may be due to the geomorphology of the watercourse, and its influence on the biological, physical, and environmental

factors such as dispersal, stream energy, discharge, stream width, slope, confinement of water flow, over bank flow, flooding, bank morphology, and availability of suitable habitats for establishment (Malanson 1993; Gurnell 1997; Cooper et al. 2003).

This study is of *Dioscorea oppositifolia*, which invades pristine stream corridors such as Giant City State Park and the Lusk Creek Wilderness Areas of Illinois (Beyerl 2001). Dispersal of vegetative propagules is primarily by gravity and secondarily by hydrochory (Yatskievych 1999; Thomas et al. 2005), so that the species has great potential for downstream dispersal and invasion once established upstream, depending on the potential for establishment in various habitats and the longevity of propagules. The longevity of seed or propagule banks is a critical issue in the spread of invasive species (Lonsdale et al. 1988; Bebawi and Row 2001; Renne et al. 2001; Holmes 2002; Yamashita et al. 2003). Invasive species with long-lived seed or vegetative propagule banks may be difficult to control in infested habitats (Leck and Leck 1998; Gibson et al. 2002) because the removal of the adult individuals will not remove viable propagules that could reinfest the habitat after management (Groves 1989).

Certain natural environments may be more conducive to the long-term storage of propagules than others, so that manipulations of the environment could be useful in the reduction of propagule banks of invasive species. For example, thick peat or litter layers can slow or prevent the germination of certain species (Bruggink et al. 1993), so that ultimately propagules deposited in thick layers of litter or peat may be maintained longer in propagule banks (Holmes and Cowling 1997). In the case of invasive species, this may mean that the potential period for invasion could be extended by the presence of litter. Therefore, management to reduce litter amounts could remove an environmental factor that would otherwise extend the retention time of viable propagules. The mechanism for the extended retention time of propagules in the presence of litter could be a more hospitable storage environment (e.g., shaded, less desiccation). After germination, litter could also provide a slow release of nutrients, which could facilitate invasion (Davis et al. 2000) and support young plants.

The objectives of this study were to document the distribution and growth patterns of *D. oppositifolia* in relationship to stream and floodplain structure in a pristine forested watershed in Illinois, and to assess the viability of bulbils of *D. oppositifolia* over time in various micro-environments on these floodplains. Viability can be defined as the condition of a bulbil (or seed), which allows the bulbil to germinate under favorable conditions (Steiner et al. 1998). We tested the null hypothesis that bulbils of *D. oppositifolia* would have the similar lengths of longevity in all environments including above leaves, below leaves, in the creek bed, or on rocks. The results of this study can be used to determine if certain micro-environments are more or less conducive to the maintenance of vegetative banks, and to design strategies to prevent the reestablishment and spread of *D. oppositifolia* in natural plant communities.

Materials and methods

Study site

This study was conducted in a tributary of Drury Creek in Giant City State Park near Makanda, Illinois (89.188° W, 37.605° N). Populations of *D. oppositifolia* along this tributary were restricted to the floodplain (Jennifer Thomas, personal observation). Population A was along a narrow floodplain (1–5 m) situated at the highest elevation in the watershed. Directly downstream from Population A, small satellite populations of *D. oppositifolia* were observed, especially on patches of rocks with soil. Farther downstream, the wider floodplain (100 m) had larger populations than upstream (Populations B and C). Population A may have been the source of the downstream populations.

Flow in the tributary channel is intermittent throughout the year, but highest after rainfall from November to June, the season contributing the most to annual rainfall (average annual precipitation = 111 cm). The channel of the tributary typically dries in July through August except for a few deeper pools. The mean summer temperature is 24.7 °C, and the mean annual temperature is 14.3 °C, with freezing common in

the winter. Habitats within the park consist of moist woods, dry slope bluffs, xerophytic blufftops, streambanks, ponds, and old fields (Mohlenbrock 1981).

Distribution map

The locations of Populations A and B were surveyed using a total station from May 2002 to 2003. Control points along the tributary were based on the known elevation of a bridge on Springer Ridge Road. Cross sections of the creek were surveyed at every bend of the creek bed. Cross sections of the creek included the top of bank, toe, edge of creek flow line, center of flow line, and a ground shoot on the opposing side of the creek channel. The spatial distribution of *D. oppositifolia* was surveyed using the parameter boundary of individuals from the top of bank onto the floodplain. Point files of the creek bed and *D. oppositifolia* locations were created and analyzed in ArcGIS Version 8.3 (ESRI 2003).

Study species

By the 1800's, *D. oppositifolia* L. was cultivated in the United States (DeBow 1869), and the species has now escaped from cultivation in 23 states, especially in the eastern United States (U.S.D.A. 2003). *D. oppositifolia* was not found in Illinois until the 1980's, when it was discovered in a natural area in Jackson County (Mohlenbrock 1986). Subsequently the species has spread to habitats in 21 counties in Illinois (Basinger 2001), including pristine wilderness canyons (Beyerl 2001).

 Dioscorea oppositifolia invades new habitats via bulbil dispersal (Thomas et al. 2005). In this species, bulbils are vegetative axillary tubers that resemble small potatoes (generally tip-of-the-thumb sized or smaller; Coursey 1967), which reach maturity on the mother plant from June through October (Okagami and Tanno 1991). Bulbils are dispersed by water in stream corridors (Thomas et al. 2005), and could be forming banks for future reestablishment, dispersal and invasion in floodplains. *D. oppositifolia* has not been observed to produce female flowers or seed in North America (R. Mohlenbrock,

personal communication), so that transmission by seed is not likely. After establishment, the species becomes a perennial vine with underground tubers of up to 1 m in length (Coursey 1967).

Bulbil longevity study

Bulbils of *D. oppositifolia* were collected along Landreth Road, near Population C of the field study. Twenty-five of the collected bulbils were placed in each of 156 bags constructed of 1 mm mesh screen. In January 2002, mesh bags containing bulbils were placed within Populations A, B and C in a randomized block design in three replicated sets within four environments (treatments) including over the leaves, under the leaves (2 cm), in the stream bed, and on bare soil. At monthly intervals for 13 months, one bag was removed from each replicate set. In the lab, bulbils were washed with tap water and rinsed with distilled water. Bulbils were tested for viability with 2,3,5-triphenyl tetrazolium (Baskin and Baskin 1998). A comparison of the germination of boiled vs. unboiled bulbils with responses to the tetrazolium test showed that tetrazolium could detect bulbil viability (Thomas 2004).

Stem growth and bulbil production

A total of 50 plots, 16 for Population A and 17 for Populations B and C were selected. Within each plot (1 m^2), one individual of *D. oppositifolia* was selected using a stratified random approach to monitor stem growth and bulbil production. The distance to the creek was measured for each tagged individual. Several features of individuals were monitored approximately every 20 days (late April, late May, late June, early August) including vine length of the dominant (longest) stem, number of bulbils per meter of stem, numbers of flowers and/or fruits per individual, and growth stage. The growth stages of *D. oppositifolia* include the Type I stage (short, single leaved and low frequency of bulbils) or the Type II stage (longer vines with many bulbils; Beyerl 2001).

Species composition and habitat characterization

In the 50 plots established for the monitoring of stem growth and bulbil production of *D. opppositifolia*, species composition and habitat were also characterized. For comparison, 50.1 m^2 plots were randomly selected and sampled, which were unoccupied by *D. oppositifolia*. Percent canopy cover of species in the plots was estimated using a Daubenmire scale (Daubenmire 1959). To characterize the habitat within each plot, canopy cover and light intensity were measured using a spherical densiometer and LiCor LI-191SA Line Quantum Sensor, respectively. Light intensity was measured as a proportion of full light outside of the forest as compared to within the plots. Slope and aspect were measured with the clinometer of a compass (Silva). Potential annual direct incident radiation (potential radiation) was calculated from slope, aspect, and latitude of the plots (McCune and Keon 2002). Soil pH was taken in the field using a soil pH and humidity tester (Takemura Electric Works, Ltd., Tokyo, Japan). Soil samples were also collected from each plot using a soil corer. Soil samples from each plot were kept in separate plastic bags and stored in a cold dark room until analyzed for moisture, and texture. Moisture content was determined by oven drying 6–8 g of each soil sample at 80 °C for 24 h. Percent moisture was calculated from the weight of the soil before drying and the weight after drying. Soil samples were dried, sieved, and analyzed for texture using the hydrometer method (Allen et al. 1974).

Data analysis

To create a distribution map, the point files of the positions of the creek flow line and individuals of *D. oppositifolia* were overlain on a digital orthophoto quadrangle (DOQ) falsely colored by a Landsat satellite scene, and a digital elevation model (DEM) with shaded relief using ArcGIS 8.3 (ESRI 2003). These layers were obtained from the USGS Terraserver (Terraserver USGS 2004). Distance to creek was calculated for each plant in the source and sink populations based on the Natural Breaks classification system using five classes using ArcGIS 8.3 (ESRI 2003). Plant distribution points and surveyed cross section points of the creek were overlain on a 10 m DEM to create a 3D image of the spatial distribution of Population B and landscape structure.

For the bulbil longevity study, regression analysis was used to test mean differences in the viability of bulbils using the main effects of environment, time and the interaction of environment×time (SAS 1999). Because there was a significant interaction of the main effects, second order polynomial curves were fit to the viability data over time for each environment, and differences in the curves and intercepts between environments were tested using Proc GLM (SAS 1999). Pairwise comparisons were made of the intercepts and shapes of the second order polynomials to examine differences in the magnitude and pattern of viability loss over time (SAS 1999).

To estimate growth rate, stem lengths of *D. oppositifolia* plants were measured approximately every 20 days at four intervals during the 2001 and 2002 growing seasons starting in late April until August (late April, late May, late June, early August).

Relative growth rate (RGR) was calculated for the fifty tagged plants measured in 2002 as:

$$\text{RGR} = \log_e L_2 - \log_e L_1 / T_2 - T_1$$

where L_1 is the length of the stem at T_1 (beginning of interval), and, L_2 is the length of the stem at T_2 (end of interval). $T_2 - T_1$ is the difference in time of measurement (20 days) (Gibson 2002). Repeated measures ANOVA was used to analyze relative growth rate over the four time intervals. One-way ANOVA was used to analyze the independent variable distance to creek and the dependent variable mean relative growth rate (SAS 1999). Mean number of bulbils produced from each of the 50 individuals in the study plots was estimated.

T-tests were used to compare the species richness (number of species) and percent cover (abundance) of plots occupied and not occupied by *D. oppositifolia*. To characterize habitat characteristics and species abundance, Principal Components Analysis (PCA) was performed using PC-ORD Version 4 using a correlation matrix of the environmental variables (McCune and Grace 2002). Parallel analysis (PA) was used to determine the number of axes to retain for interpreta-

tion (Franklin et al. 1995). Axis one, two, and three (eigenvalues 3.05, 1.89, 1.38) of the PCA were retained for interpretation. Spearman rank correlation was used to determine the relationship between the gradients in environmental variability (i.e., PCA axes scores for plots with *D. oppositifolia*), and the abundance of *D. oppositifolia*, and the three other co-occuring invasive species (*Euonymus fortunei*, *Lonicera japonica*, and *Rosa multiflora*).

Results

Distribution of D. oppositifolia in the floodplain

At the highest elevations in the watershed, Population A (37°36′50″ W, 89°11′38″ W, elevation

172.8 m) was confined to within 6.9 m from the center of the creek bed (Figure 1), which was rocky with high banks. Water flow in the creek bed near Population A was rapid during heavy rain events, with little woody debris deposition. Population B (37°37′34″ N, 89°12′22″ W, elevation 125.9 m) had a greater distribution of *D. oppositifolia* in a wider floodplain and was 1.4 km downstream from Population A (Figure 1). A large number of individuals were in the creek bed and on the top of the bank, 0–6.9 m from center of the creek (Figure 2). On the north side of the creek, the population of *D. oppositifolia* was distributed up to 29.0 m from the center of the creek bed, with some individuals abutting tall sandstone bluffs at the edge of the floodplain. The south side of the
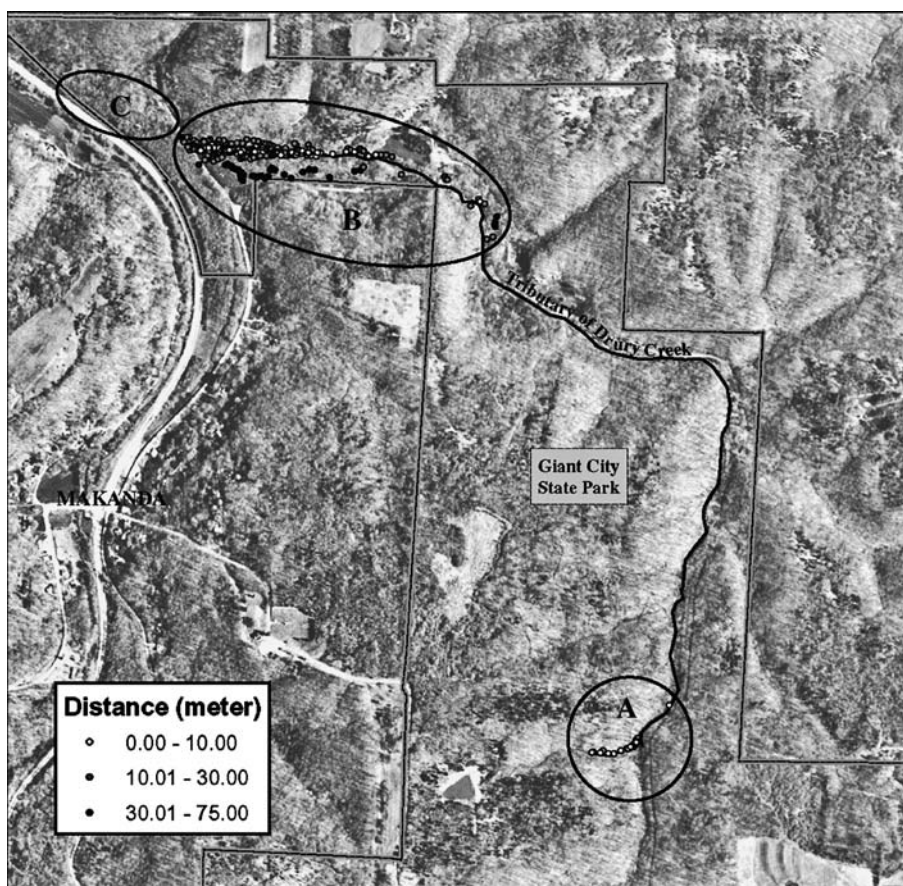

Figure 1. Distribution of *D. oppositifolia* populations along the tributary of Drury Creek in Giant City State Park, southern Illinois. The creek flows from the upland Population A (source) to the lowland Populations B and C (sinks).

creek had the widest distribution of *D. oppositifolia* in the floodplain (up to 73.9 m from the center of the creek bed; Figures 1 and 2). The floodplain beyond 74 m from the center of the creek bed was inundated with water during winter months, and had few individuals of *D. oppositifolia* (Jennifer Thomas; personal observation). Population C was 20 m downstream from Population B and individuals of *D. oppositifolia* were distributed beyond the survey areas outside of Giant City State Park (37°37′37″ N, 89°12′32″ W, elevation 125.9 m). The actual distribution of this Population C was not mapped, but a general area of distribution was drawn based on visual observation (Figure 1). In the lowland Populations B and C, the creek bed was sandy and carried small rocks, sand, woody debris and litter after heavy rainfall events. Drift lines of debris occurred in the floodplains along the banks of the creek in these lowland populations, especially on the south side of the creek (personal observation).

Relative stem growth and bulbil production

Relative stem growth differed for *D. oppositifolia* during various time intervals ($F_{3,180} = 219.5$, $P < 0.0001$) during the 2002 growing season. Relative growth rate was lower in the late-May survey than in the late April survey and lower in the mid-June survey than in late-May, but not different in late-June and early August (Figure 3). Relative growth rate was not related to the distance of individuals from the creek ($F_{44,1} = 0.18$, $P = 0.98$).

Only 18 out of the 50 tagged individuals of *D. oppositifolia* produced bulbils. These individuals produced a mean of $14.8 \pm SE$ 1.7 bulbils per
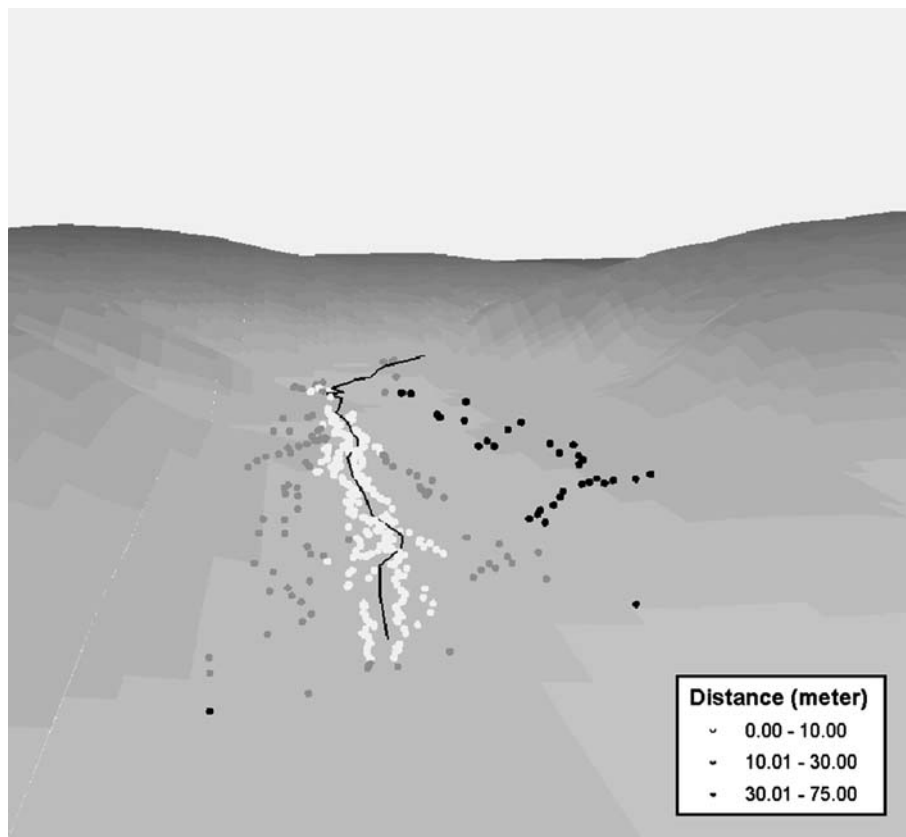

Figure 2. 3D map showing landscape structure and distribution of *D. oppositifolia* plants in Population B along the tributary of Drury Creek. Population B is east of Springer Ridge Road in Giant City State Park. Distance represents the location of individual plants in relation to the middle of the creek.
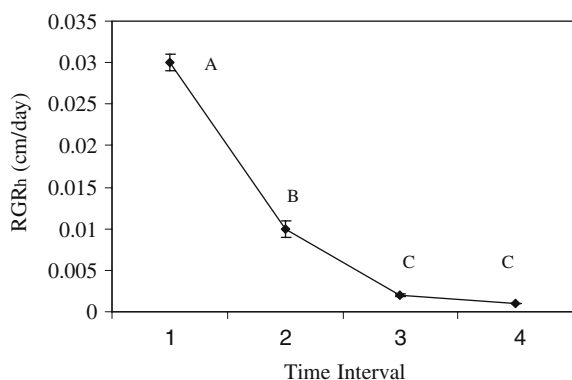
Figure 3. Mean (±1 SE) relative growth rate (RGR) of individuals of *D. oppositifolia* from April to August 2002 (time interval 1: late April; interval 2: late May; interval 3: late June; interval 4: early August). Means with the same letter are not significantly different at α = 0.05.

Species richness did not differ between plots occupied and not occupied with *D. oppositifolia* (species richness: 4.06 ± 0.11 vs. 4.02 ± 0.13 species, respectively; $t = 0.47$, DF = 98, $P = 0.64$). The percent cover of species differed in plots occupied and not occupied by *D. oppositifolia* ($t = -4.54$, DF = 98, $P < 0.0001$). The percent cover of native species was significantly higher in plots unoccupied than in plots occupied with *D. oppositifolia* (91.2 ± 2.7 vs $70.3 \pm 3.7\%$, respectively). Some native species occurred with *D. oppositifolia* in the low elevation sites including *Laportea canadensis* (wood nettle) and *Arundinaria gigantea* (giant cane). Invasive species that occurred with *D. oppositifolia* included *Euonymus fortunei*, *Rosa multiflora*, and *Lonicera japonica*. However, these species do not invade or regenerate via asexual propagules in a manner similar to that of *D. oppositifolia*.

Species composition and habitat characterization

Plots occupied and unoccupied with *D. oppositifolia* were not distinctly separate from one another in the ordination figure of the PCA except for plots within Population A (Figure 4). Axis 1 was related to soil texture, light and slope (cumulative % of variance = 33.87%; Table 1). Axis 1 was also related to the presence of *D. oppositifolia*
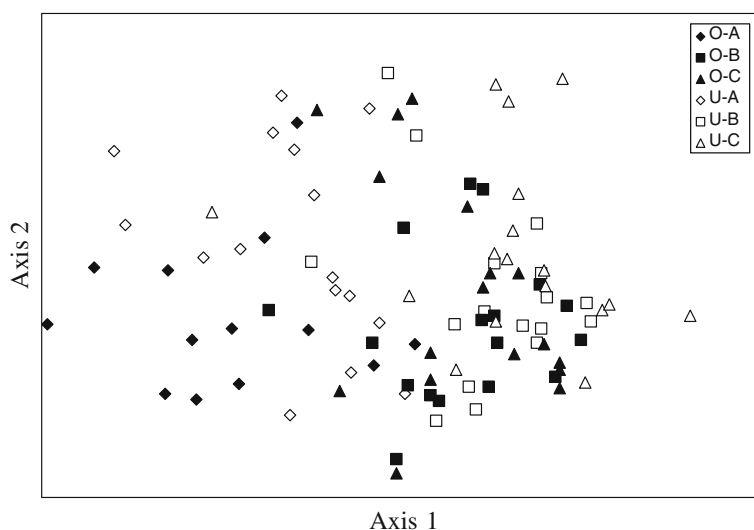
meter of stem, and only 46 of the 50 individuals survived for the entire growing season. Four of the 46 surviving individuals were Type I, and 42 were Type II, which produced bulbils. Flowers and fruits were not produced on the 46 surviving tagged plants. Male flowers were observed on one Type II plant growing on a sign in full sunlight on Springer Ridge Road near Population B. No female flowers were observed during the study.

Figure 4. Principal Components Analysis (PCA) ordination of habitat variables measured in plots occupied (O) and unoccupied (U) by *D. oppositifolia* in Populations A, B, and C including (a) Axes 1 and 2.

($r = 0.497$, $P = 0.0003$) but not with other invasive species such as *Euonymus fortunei*, *Rosa multiflora* and *Lonicera japonica* ($r = 0.207$, 0.0812 and -0.130, respectively; $P = 0.154$, 0.577, 0.377, respectively). Soils in the plots in Population A with *D. oppositifolia* had higher percentages of sand while unoccupied plots had higher percentages of silt. Axis 2 was related to slope and light (cumulative % of variance = 54.86%). A majority of the plots with low potential radiation were on higher, north facing slopes while the plots with higher potential radiation were on lower, south-west facing slopes. Axis 3 followed a moisture and canopy gradient (cumulative % of variance = 70.19%; Table 1). Along Axis 1 and 3, plots with lower % canopy coverage had higher soil moisture. When comparing Axes 2 and 3 (Figure 4 not shown), plots with higher soil moisture had higher potential radiation and lower slopes. This suggests that soil moisture was higher in plots with lower canopy, higher potential radiation, and lower slope, and may be associated with lower gradient floodplain environments.

Individuals of *D. oppositifolia* were distributed across the environmental gradients represented by the ordination. The habitat mainly consisted of sandy loam soil with a mean pH of 6.6, 21% soil moisture, and a 5° slope. Mean % canopy cover was 71%, mean light intensity was 6%, and mean potential radiation was 0.9 mol m^{-2} s^{-1}.

Bulbil viability and environment

The pattern of bulbil viability varied over time in different environments (i.e., environment×time interaction; $F_{3,144} = 2.03$; $P < 0.0031$). The pattern of viability loss over time did not vary under leaves, in the creek, or in the soil (1 d.f. con-

trasts: $F = 0.09$–0.55, $P = 0.46$–0.76, Figure 5), however, for bulbils placed over leaves, the pattern of viability loss differed in shape over time from the other treatments ($F = 7.4$–9.2; $P < 0.008$–0.004; Figure 5). More viable bulbils were maintained under leaves over time, i.e., the intercept of the equation for viability over time was higher under leaves vs. in the creek and in the soil ($F = 15.7$, $P < 0.0002$ and $F = 15.8$, $P < 0.0002$, respectively; Figure 5; mean bulbils viable = 76.0 ± 6.8, 21.2 ± 9.6, 21.6 ± 3.6, and 5.2 ± 5.2%, respectively). We observed that bulbils placed in the mesh bags germinated during the growing season from April through November 2002.

Discussion

The spread and ultimate pattern of distribution of a species will be influenced by the interconnectivity and availability of suitable habitats for establishment within the landscape (With 2002). Colonization patterns of plant species in riparian systems often are restricted to portions of the floodplain with overbank flooding (Hupp and Osterkamp 1985; Walker et al. 1986; Thebaud and Debussche 1991; Hampe 2004). Similarly, the distribution and spread of *D. oppositifolia* in Giant City State Park is related to the interplay of floodplain environment and overbank flow in the creek. *Dioscorea oppositifolia* is restricted in the upper watershed near Population A, where creek flow velocity is rapid and the narrow floodplain is abutted by steep embankments. As the creek decreased in elevation near Populations B and C, the floodplain widened, and the available habitat for *D. oppositifolia* expanded. In the

Table 1. Eigenvectors of habitat variables for Axes 1, 2, and 3 of the PCA.

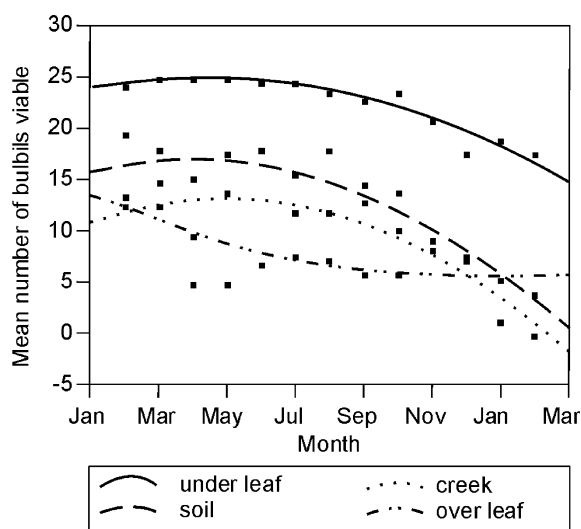| Habitat variables	Eigenvector (Axis 1)	Eigenvector (Axis 2)	Eigenvector (Axis 3)
Sand (%)	-0.48	-0.17	-0.31
Clay (%)	0.07	0.32	0.19
Silt (%)	0.48	0.10	0.29
Moisture (%)	-0.04	-0.14	0.62
pH	-0.10	-0.22	-0.35
Canopy cover (%)	0.41	0.24	-0.36
Light (%)	-0.39	-0.24	0.37
Potential radiation	0.31	-0.58	-0.04
Slope (°)	-0.32	0.58	0.04

Figure 5. Mean (±1 SE) number of viable bulbils per mesh bag of *D. oppositifolia* in four environments (under leaves, over leaves, in the creek, and in soil) over time from February 2002 to 2003 in a forested watershed in Illinois. Twenty-five bulbils were initially placed into each mesh bag.

lowland areas at Population B and C, overbank flooding with deposition of bulbils and other debris occurs during rainstorms (Thomas et al., 2005). Throughout this watershed, *D. oppositifolia* was most common in the flattest part of the floodplain with sandy loam soil, and low levels of light. Another study in southern Illinois found that *D. oppositifolia* does not occur in silty loam (Beyerl 2001), presumably because the underground tubers rot in soils with poor drainage (Coursey 1967). Thus, the distribution of *D. oppositifolia* is limited to the portion of the floodplain with well drained soils, but with episodes of flooding to promote the dispersal and deposition of bulbils, which likely originate from upstream sources.

In another study, the distribution of the invasive *Fraxinus ornus* along the Herault River in southern France was related to geomorphologically-related features such as flooding, long distance dispersal by hydrochory, and availability of suitable habitats, and these same features fostered the rapid range extension (970 m year^{-1}) of this species (Thebaud and Debussche 1991). Similarly, the dispersal and the structure of the floodplain at Giant City State Park seems to be facilitating the invasion and undoubtedly the

range expansion of *D. oppositifolia* via downstream dispersal.

While the level of interconnectivity and availability of suitable habitat are undoubtedly the most important factors in the spread of invasives at the habitat or watershed scale, the suitability of micro-environments for the survival of bulbils of *D. oppositifolia* within the floodplain constrain the species distribution at the local scale. Thus, abiotic constraints on invasion success differ at these two scales. Studies that consider a single scale of analysis may miss potentially important limiting factors.

This study found that bulbils of *D. oppositifolia* have various lengths of longevity depending on the type of micro-environment onto which the bulbils were deposited. More than 60% of the bulbils remained viable for more than 1 year when placed under leaves, but not in other environments (on top of leaves, on rocks, on bare soil; Figure 1). Under leaves, the succulent bulbils of *D. oppositifolia* were likely to be more protected from environmental factors that might kill the bulbils than in other environments. While we did not test this idea *per se* for bulbils, other studies have linked litter with increased viability of seeds (Bruggink et al. 1993; Johnson and Fryer 1996; Holmes and Cowling 1997). Based on these studies of seeds, the environmental factors that could be ameliorated for bulbils by litter include predators, fire, desiccation, and freezing temperatures. It is likely that all of these factors affect the viability of bulbils. Note that we have observed that predators often do not kill bulbils (e.g., squirrels; J. Thomas, personal observation) because bulbils can germinate as long as at least 34% of the bulbil remains uneaten (Beyerl 2001). Nevertheless, litter could play a role in camouflaging bulbils so that they are less detectable by such predators.

Knowledge of the longevity of invasive species in various micro-environments can help managers design approaches to the control invasives (Holmes and Cowling 1997; Renne et al. 2001), particularly because the seeds and vegetative propagules of invasive species can form an available source of material for reinvasion (Lonsdale et al. 1988; Bebawi and Row 2001; Renne et al. 2001; Holmes 2002; Yamashita et al. 2003). Our results suggest that reducing the leaf litter in

habitats already invaded by *D. oppositifolia* could reduce the load of bulbils harbored in the leaves.

Fire is a management option, because of its potential in removing leaves and bulbils harbored within them. The US Forest Service has burned the floodplain area of the creek in a nearby wilderness canyon (Lusk Creek Wilderness Area), in an attempt to control *D. oppositifolia* (J. Schimp, personal communication), but no monitoring results are available from this work. Other studies have shown that burning sometimes destroys seeds, thereby reducing the viability of invasive species, e.g., fire kills the seeds of *Chromolaena odorata* (Mbalo and Witkowski 1997). However, we do not know if fire kills the bulbils of *D. oppositifolia*, nor do we have any direct evidence that burning will reduce the spread of *D. oppositifolia*.

Acknowledgements

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