Journal of the Torrey Botanical Society 132(2), 2005, pp. 187–196

Water dispersal of vegetative bulbils of the invasive exotic *Dioscorea oppositifolia* L. in southern Illinois[1]

Jennifer R. Thomas[2] **and David J. Gibson**[3]
Southern Illinois University, Department of Plant Biology, Carbondale, IL 62901-6509

Beth A. Middleton
USGS National Wetlands Research Center, Lafayette, LA 70506

THOMAS, J. R., D. J. GIBSON (Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901-6509), AND B.A. MIDDLETON (National Wetlands Research Center, Lafayette, LA 70506) . Water dispersal of vegetative bulbils of the invasive exotic *Dioscorea oppositifolia* L. in southern Illinois. J. Torrey Bot. Soc. 132: 187–196. 2005.—Riparian corridors promote dispersal of several species of exotic invasives worldwide. Dispersal plays a role in the colonization of exotic invasive species into new areas and this study was conducted to determine if the invasiveness of *Dioscorea oppositifolia* L. (Chinese yam) is facilitated by secondary dispersal of vegetative diaspores (bulbils) by water. Since seed production of this plant has not been observed in the United States, bulbils represent the only means of dispersal to new habitats. Dispersal was monitored by placing aquatic traps, tethered bulbils, and painted bulbil caches in a tributary of Drury Creek, Giant City State Park, Illinois. Results indicate that high-energy flow in the creek accelerated secondary dispersal of bulbils downstream and onto the floodplain. The longest recorded dispersal distance was 206.2 m downstream. Dispersal distance of tethered bulbils was not related to rainfall or flow velocity in the creek; however the total number of bulbils trapped was positively related to flow velocity. We conclude that secondary dispersal by water in streams can facilitate dispersal of vegetative bulbils of this exotic species.

Key words: bulbils, *Dioscorea oppositifolia*, exotic species, invasive species, saltation, water dispersal.

Successful invasion by plants includes their reproductive (Drake et al. 1989) and dispersal ability (Cronk and Fuller 2001, Pyšek and Prach 1994) coupled with the ability to make efficient use of available resources (Davis et al 2000, Thompson et al 2001, Kolb et al. 2002). Characteristics of successful plant invaders include vigorous vegetative reproduction and modes of secondary dispersal that may significantly enhance the distance propagules may disperse through primary dispersal (Baker 1965, Ozinga et al. 2004). During the process of plant invasion, high energy dispersal by water can accelerate diffusion of vegetative diaspores (Thebaud and Debussche 1991). Streams and riparian zones along streams can accelerate dispersal by providing corridors in the landscape (Parendes and Jones 2000, Boedeltje 2004, Boedeltje et al. 2003). In addition to terrestrial routes, invasive plants can disperse up or down stream in riparian corridors (DeFerrari and Naiman 1994, Cooper et al. 2003), as well as the overflow zone on the floodplain from the high water mark to the center of the stream (Naiman et al. 1993). These corridors are diverse, dynamic and complex habitats (Naiman et al. 1993) that are vulnerable to invasion because of disturbance and landscape structure (Malanson 1993). Riparian corridors exhibit high energy water flow with flooding and erosion of stream beds and banks, which creates a diverse habitat mosaic with the deposit of sand, gravel, mud, woody debris and litter (Malanson 1993). Species that invade along riparian corridors are adapted to these conditions.

There are several important stages in plant invasion: introduction and survival, stabilization through reproduction, and colonization by dispersal to new areas. For an exotic species to become invasive, it must overcome the physical, chemical, and biological barriers of its new environment (Gray et al. 1987, Hierro et al. 2005). Two of the greatest barriers for water-dispersed species are the transfer of bulbils or seeds from source populations to sites of deposition and establishment (Ashton and Mitchell 1989). Typically, the success of dispersal depends upon the duration of the buoyancy of diaspores and the amount of time spent in water (Schneider and Sharitz 1988). The floatation time of diaspores gives insight into the long-distance dispersal potential of species (Darwin 1855). Diaspores with

---

[1] This research was supported by the Illinois Department of Natural Resources. We thank Heidi Hartman, Eric Johnson, Nicholas Susnis, and Al Dzurny for field and lab assistance.

[2] Current address: 4500 Shaw Boulevard, Monsanto Research Center, St. Louis MO 63110.

[3] Corresponding author: E-mail: dgibson@plant.siu.edu

Received for publication May 24, 2004, and in revised form November 8, 2004.

high buoyancy are most frequent along rivers; however, successful hydrochores (water dispersed diaspores) are not always adapted for water dispersal. Diaspores that are not buoyant are not as heavy as stones, and while too dense to float, may be still dispersed over vast distances by water flow (Malanson 1993). It is important to measure dispersal of propagules, because morphology alone may lead to incorrect assumptions regarding a species' dispersal mechanism (Johansson et al. 1996, Vellend et al. 2003).

There are many cases of exotic plant invasions along riparian corridors. For example, *Fraxinus ornus* has invaded the Herault River in southern France (Thebaud and Debussche 1991). Several invasive plant species have spread along streams in the H.J. Andrews Experimental Forest in Oregon (Parendes and Jones 2000), in northern Sydney, Australia (King and Buckney 2000) and the Adour River in France (Decamps et al. 1995). Other examples of invasive riparian plants around the world are: *Impatiens glandulifera*, *Reynoutria japonica*, *Reynoutria sachalinensis*, *Crassula helmsii*, *Fallopia japonica* (Europe), *Heracleum mantegazzianum* (Czech Republic), *Tamarix chinensis*, *Elaeagnus angustifolia*, *Eucalyptus* spp., *Ulmus pumila*, (southwestern United States) (Sauer 1988, Malanson 1993, de Waal et al. 1994), *Fallopia japonica* (eastern United States) (Forman and Kesseli 2003), *Ricinus communis*, *Nicotiana glauca*, *Sonchus oleraceus*, *Xanthium spinosum*, *Argemone ochroleuca*, and *Mimosa pigra* (Australia) (Sauer 1988).

Study Species. *Dioscorea oppositifolia* L. (syn. *D. batatas* Decne., *D. divaricata* Blanco., *D. opposita* Thunb., Chinese yam, cinnamon vine), an invasive riverside plant in the United States, is the subject of this study. *Dioscorea oppositifolia* has escaped from cultivation in twenty-three states in the eastern part of the United States (USDA 2003) and is a serious threat to native plant species richness and abundance, threatening biodiversity throughout its introduced range. A number of agencies list *D. oppositifolia* as a problematic invasive, for example, the Southeast Exotic Pest Plant Council's Invasive Exotic Pest Plant List for Tennessee includes it as a Rank 1-Severe Threat species (Tu 2002), and Illinois has established a Chinese Yam Task Force (J. Shimp, pers. comm.).

Dioscorea oppositifolia is cultivated and native in parts of North China, Korea, and central and northern Japan (Okagami and Tanno 1991). *Dioscorea* species were introduced to the United States in the 1800's as ornamental and food crops (DeBow 1869). *Dioscorea oppositifolia* was cultivated during the mid-nineteenth century in France, Germany, England, and Ireland as an alternative crop due to potato blight (Coursey 1967). Many native Chinese plants were first introduced to the United States indirectly from other countries (Lancaster 1989). During the nineteenth century, *D. oppositifolia* was also introduced to Hawaii by Japanese immigrants (Coursey 1967). *Dioscorea oppositifolia* was brought to the United States mainland from Hawaii in 1913 for use as an ornamental plant (Hawley 1956) and in 1921 from England and France (A. K. Stoner, pers. comm.). Advertisements from the early 1900's promote *D. oppositifolia* as a beautiful, hardy climbing vine (Lippincott 1909,1913).

In Illinois, the first noted appearance of an escaped population of *D. oppositifolia* from cultivation was in Jackson County, southern Illinois (Mohlenbrock 1986). Subsequently, Basinger (2001) found escaped populations of *D. oppositifolia* in thirteen counties in southern Illinois and indicated reports of populations in eight additional counties. Many populations of *D. oppositifolia* in Illinois are found near streams and in some of the regions's most highly prized natural areas such as the Lusk Creek Wilderness Area and Giant City State Park (Gillespie 2003). In these areas, *D. oppositifolia* appears to invade riparian corridors from an initial colonization site in the upper reach of a headwater tributary (Bassinger 2001).

Dioscorea oppositifolia is a perennial vine that emerges in late April or May. This species produces two types of tubers: underground tubers up to 1 m in length and smaller axillary tubers (bulbils), which resemble small potatoes (Coursey 1967). These bulbils are vegetative propagules, which usually are present on the plant from June–October. Bulbils increase in size, maturity and level of dormancy while attached to the mother plant and reach full maturity in October before dispersal (Okagami and Tanno 1991). At the time of dispersal, the leaves of the mother plant wither. *Dioscorea oppositifolia* is dioecious but in its current range in the United States, including southern Illinois, plants are all staminate, so no seed production has been observed (Tu 2002), and *D. oppositifolia* appears to be spreading only by production of asexual bulbils. Primary dispersal of the bulbils is by gravity, but they can disperse secondarily via hydrochory (water dispersal) (Yatskievych 1999). Beyerl (2001) indicated that bulbils have a short primary dispersal distance of around 10 m. If longer distance secondary dispersal is significant for this species, it would be likely by water given its riparian habitat. Nevertheless, immature bulbils are denser than water and while mature bulbils are somewhat lighter this is not an obvious adaptation to dispersal by flood waters (Coursey 1967).

It is not known if the invasiveness of *D. oppositifolia* is facilitated by secondary dispersal by water. It spreads along riparian corridors yet its vegetative propagules do not float in water. Knowledge of the extent to which bulbils can move downsteam by water, thus accelerating invasion, is lacking, but would assist in the development of management strategies for this species. The objective of this study was to describe dispersal patterns of bulbils of *D. oppositifolia* and to assess the potential of bulbils to disperse downstream in riparian corridors and watersheds.

Materials and Methods. STUDY SITE. The study site was the watershed of Drury Creek in Giant City State Park, 89.188° W, 37.605° N, Shawnee National Forest, Illinois. The park has massive sandstone cliffs and intermittent rocky streams (Mohlenbrock 1981). Habitats within the park consist of moist woods, dry slope bluffs, xerophytic blufftops, streambanks, ponds, and old fields, but *D. oppositifolia* is restricted to the stream corridors (Thomas 2004). The average growing season is 187 days with the first killing frost around October 24th and the last April 10th (Mohlenbrock 1981). The average annual precipitation is 111 cm, with the majority of the rainfall occurring between November through June (Fig 1). July and August are the driest months of the year despite occasional thunderstorms.

This study of bulbil dispersal was conducted along the corridor of a tributary of Drury Creek, which originates near the tops of hillsides. At the highest elevations the tributary has a smooth rocky bottom, while at the lower elevations the creek bottom becomes sandy. Flow in the tributary is intermittent throughout the year, but it is highest after rainfall in November to June. The tributary typically becomes dry in July through August except for a few deep pools. The channel carries small rocks, sand, woody debris and litter after heavy rainfall and these are deposited along the banks and in the floodplain (Thomas, personal observation). In the lowland areas, flooding or over-bank flow may occur (Mohlenbrock 1981). Several stands of *D. oppositifolia* grow along this tributary of Drury Creek including a small stand in the upland area that will be referred to as "stand A" (37° 36′ 50″ W, 89° 11′ 38″ W, elevation 172.8 m). The creek bed near stand A is rocky with high banks, and during heavy rain water flow in this portion of the creek bed is rapid with little woody debris. Downstream from this area there are a few patches of *D. oppositifolia* along the creek banks, and as the creek decreases in elevation, its bed becomes sandy, and the stands of *D. oppositifolia* increase in size ("stands B and C"). Stand B is 1.4 km downstream from stand A (37° 37′ 34″ N, 89° 12′ 22″ W, elevation 135.5 m) and stand C is 20 m downstream from stand B and continues outside of the park (37° 37′ 37″ N, 89° 12′ 32″ W, elevation 129.1 m). Stands B and C are in the floodplain in zones of over-bank flow, large woody debris, and litter. Population density ranged from 73–116 plants ha in stands B and C to ~ 200 plants ha in stand A with highest densities occurring closest to the stream channel (Thomas et al., in press).

BULBIL DISPERSAL. Water dispersal of bulbils was monitored from October 2001–February 2003 in the three stands (A, B, and C) of *D. oppositifolia* that were growing adjacent to the stream. Estimates of bulbil dispersal were obtained using two types of traps, counts of bulbils trapped in stream debris, and by monitoring bulbil movement directly. We used several methods because dispersal of *D. oppositifolia* bulbils has not been monitored previously. Our goal was to obtain minimum estimates of bulbil movement and relative densities at different times of the year, rather than accurate densities.

Aluminium traps were placed among the plants of *Dioscorea oppositifolia* in each stand. The aluminium traps were made from aluminum pie pans (21.6 cm diameter × 3.3 cm depth) covered with a plastic ~ 2.5 cm diamond mesh. Heavy weight aluminum foil was painted with Tanglefoot® (a sticky substance typically painted on trees as a pest barrier) and placed in the bottom of the traps (Kollman and Goetze 1998, Middleton 1995). A 56.7 g weight was tied with fishing wire to the bottom of each trap. Every month the traps were monitored for bulbils, and the foil painted with Tanglefoot® was replaced. Aluminium traps were placed 1 m apart along

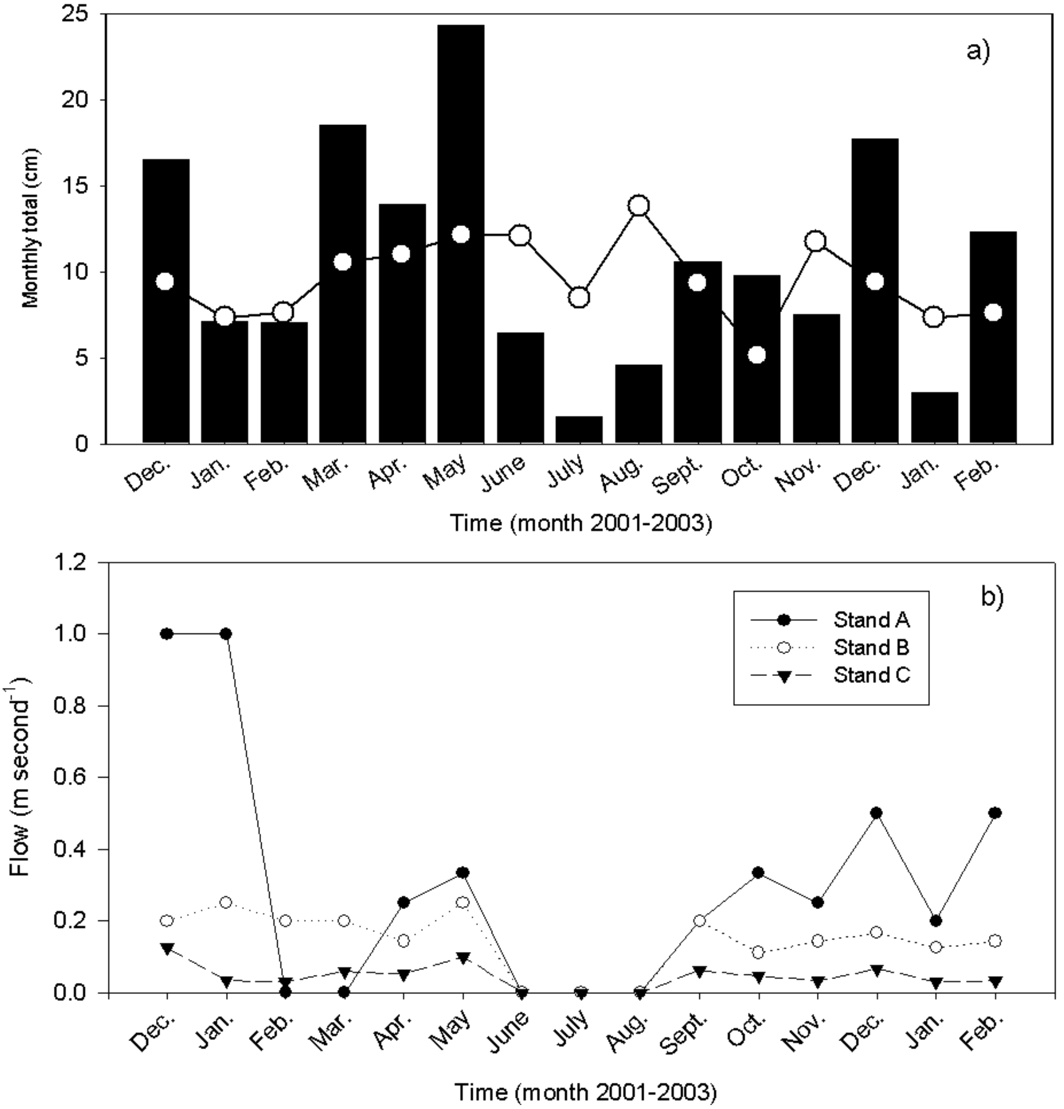

FIG. 1. a) Monthly total precipitation (cm) during the study period (bars) and long-term average (line, 1948–2002) (source: NOAA, Carbondale Sewage Plant), b) Stream flow (m sec^{-1}) in three stands of *Dioscorea oppositifolia*. Note: the stream was dry from June through August 2002.

three transects running from one side of the creek to another. The three transects were positioned perpendicular to the creek bed and their locations relative to the center of the stream were chosen randomly by drawing a number between 1 and 30. One transect was placed within each of the three populations, close to the downstream boundary of each. Within each transect, 5 traps were placed 1 m apart and secured with nylon rope across the creek bed, with two additional traps placed on the streambank.

Bucket traps were modified from Middleton's (1995) aquatic trap design to measure hydrochory in rivers. These traps were made of plastic buckets (27 cm circumference) in which the bottoms and lid rims had been removed with a jigsaw. A cloth bag was attached inside the bucket. Ten of the buckets traps were tied across the creek in each stand in June 2002. The traps floated with the fluctuating water level and were monitored for the presence of bulbils monthly through February 2003.

Woody debris and litter were collected from the traps in the creek and from drift lines (accumulated litter, including leaves, fruits and twigs on the banks) within the 3 stands from

December 2001–February 2003. Each month during the rainy season, 0.08 m^3 of debris was collected randomly from the trap lines and from drift lines on the banks. The debris was transported to the lab and sorted by hand for bulbils as well for any other diaspores to determine species dispersing in the creek.

Bulbils collected from the traps and debris were counted, air dried and tested for viability. Bulbil viability was tested using the tetrazolium test (Grabe 1970, Thomas 2004).

Bulbil dispersal by water was measured directly using two methods; monitoring tethered bulbils and spray-painted bulbils. For these measurements, bulbils were obtained from a *D. oppositifolia* population along Landreth Road, Jackson County, Illinois, T10S R2W 34. Bulbils were tied and glued to 5 m of yarn and then tied to a tent stake or to a large rock in the creek bed (e.g., Vila and Lloret 2000). Monthly from November 2001, three bulbils were placed in each of 5 caches near the three *D. oppositifolia* stands (A, B, and C). The bulbils were placed in the creek bed with the first cache 30 m upstream from the trap line associated with the stand. Subsequent caches were placed at 5 m intervals downstream until 5 caches had been established in the stand. The bulbil caches were monitored monthly until February 2003 for movement of the bulbils. The destination of the bulbils was determined by following the yarn downstream. Bulbil dispersal distance and direction were measured from the bulbil caches.

Other bulbils were spray painted (Schneider and Sharitz 1988) and placed in caches each month from January 2002–February 2003. These bulbil caches were placed both in the creek bed and along the edge at the very top of the stream bank parallel to the caches placed in the creek bed. The caches were randomly placed on the left or right bank. In the creek bed they were again placed starting 30 m upstream from the first trap line and every 5 meters downstream thereafter. Three bulbils were placed in each of 5 caches after they were painted with different colors and numbered with a permanent marker to designate the original location of the bulbil. Bulbil disappearance, dispersal distance, and direction were measured by searching the creek bed up to 250 m below the placement of the caches.

Current speed (m sec^{-1}) in each of the three stands of *D. oppositifolia* was determined each month (Dec 2001—Feb 2003) by measuring the time it took for a floating leaf to travel one meter (Brown 1971). Monthly precipitation totals for the local area were obtained from the Carbondale Sewage Plant weather station located 10 km away (National Climatic Data Center: http://lwf.ncdc.noaa.gov/oa/ncdc.html).

Data Analysis. The total number of bulbils found in debris collected from the aluminum traps and drift lines on the banks was converted to number of bulbils per cubic meter of debris and bulbils captured in the bucket traps were converted to number of bulbils per meter squared of trap area (Middleton 1995). Mean weight (g air dry), length, width (cm), and viability were calculated for the bulbils captured in the debris and traps. Mean dispersal distance (monthly and annually), direction, and current speed were calculated for the tethered and painted bulbils. Repeated measures ANOVA in SAS Ver 8.2 was used to test the effects of month (repeated measure) and stand on dispersal distance of the tethered bulbils. Dispersal distances were log transformed prior to analysis, with untransformed values retained for presentation and calculation of mean distances. The relationship between dispersal distance of tethered and painted bulbils and the number of trapped bulbils to stream flow and rainfall was investigated using Spearman Rank correlation in SAS. Too few of the painted bulbils were recovered (19 of 180) to allow statistical analysis comparing the three stands and so simple means ± SE are presented of these data.

Results. Precipitation during the study period varied from 1.6–24.3 cm per month with a summer drought during June–August. Creek flow over this time ranged from periods of no flow in stand A during February and March when the stream was frozen, and June–August when the stream was dry, to flow rates of 1.0 m sec^{-1} (Fig 1b). Higher rates likely occurred during flooding but flow was not recorded during rainstorms, so maximum current speeds that would disperse bulbils long distance are unknown. Current speed in the upper reaches of the stream in stand A was consistently higher (mean = 0.43 ± 0.1 m sec^{-1}) than further downstream in stands B and C (means = 0.14 ± 0.02 and 0.04 ± 0.01 m sec^{-1}, respectively).

The greatest density of bulbils (75.9 m^{-3}) in debris collected from aluminum traps in the creek occurred in December 2001 (Fig. 2a). Bulbil density decreased from January to March. During June–August the creek completely dried

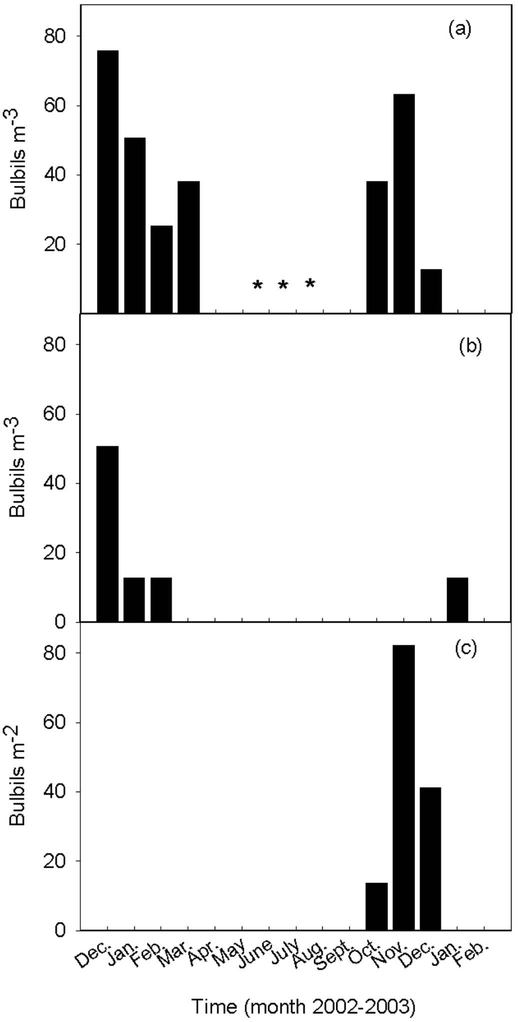

FIG. 2. Dispersal of bulbils of *Dioscorea oppositifolia* December 2001 to February 2003 in a tributary of Drury Creek, southern Illinois, a) Total number of bulbils found per m^3 of debris collected from aluminum traps in creek (n = 24 bulbils), b) Total number of bulbils found per m^3 of debris collected from drift lines along the stream banks (n = 7 bulbils), and c) total number of bulbils per m^2 captured in bucket traps (sampling from June 2002–February 2003 only) (n = 10 bulbils). * = stream dry (see Fig 1).

out, bulbils were not dispersed, and no fresh debris was available for collection. Bulbils were found again in October, increased in density in November, and then decreased in density in December 2002. Throughout the entire study, a total density of 303.8 bulbils m^{-3} was found in the debris collected from the aluminum traps in the creek.

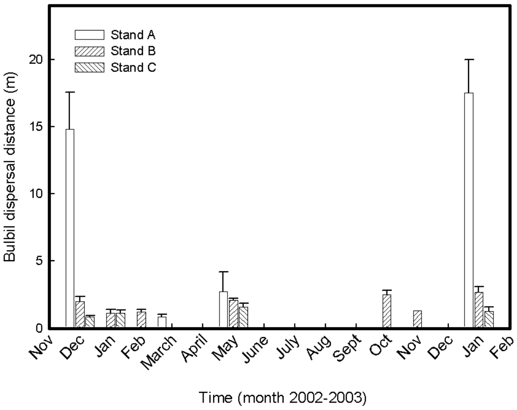

FIG. 3. Mean dispersal distance (± SE) of tethered bulbils (n = 87) of *Dioscorea oppositifolia* from 3 stands from November 2001 to February 2003.

The largest density of bulbils found in debris collected from drift lines along the banks occurred in December of 2001 with a total of 50.6 bulbils m^{-3} (Fig. 2b). In total, 12.7 bulbils m^{-3} were found the following winter months of January and February and in January the following year, but none were found in any other months. A total of 88.7 bulbils m^{-3} was found in the debris from drift lines on the banks. The bucket traps only captured bulbils in October–December 2002 (Fig. 2c). The largest number of bulbils captured in the bucket traps occurred in November 2002 with 82.2 bulbils m^{-2}, and 137 bulbils m^{-2} were captured over the entire season. All captured bulbils were viable, both from the debris and traps. Diaspores from *Quercus* spp., *Acer* spp., *Juglans nigra* L., *Gymnocladus dioicus* (L.) K. Koch., *Fraxinus americana* L., and *Carya ovata* (Miller) K. Koch. also were found in debris and traps.

Many of the tethered bulbils were washed away completely, tangled in debris, buried in sand, or frozen. Most of the bulbils placed in stand A washed away during the rainy season, along with the rocks to which they were tied. Many were lost in stands B and C as well, so mean dispersal distance was tabulated for each month based on the available measurements of dispersal distance. Repeated measures ANOVA indicated a significant interaction between month and stand ($F_{6,71} = 8.24$, $P < 0.0001$). Bulbil dispersal distance was similar between stands B and C, but dispersal distances in stand A showed large peaks in December 2002 and January 2003 (Fig 3). The longest mean distance of 4.8 m ± 2.1 occurred in January 2003 (Fig. 3). The longest measured distance recorded of an individual tethered bulbil was 20 m, which oc-

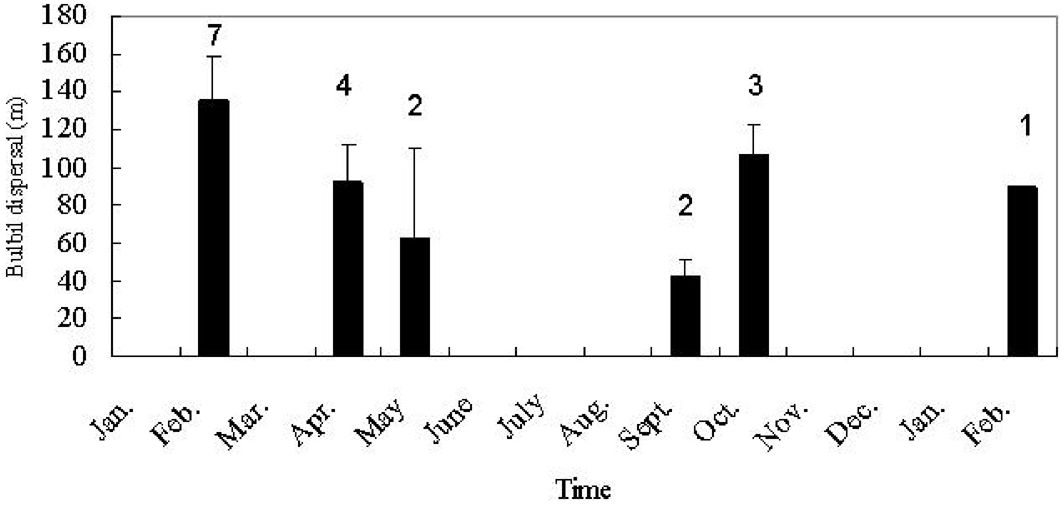

FIG. 4. Mean dispersal distance (± SE) of painted bulbils of *Dioscorea oppositifolia* placed in the creek near stand A from January 2002 to February 2003. Numbers above the bar graph represent the total number of bulbils recovered (of 180 placed out).

curred following the recovery of a bulbil that had broken free from its anchor in the creek in January 2003. Annual mean dispersal distance of all bulbils was 1.95 m ± 0.4. Bulbil movement coincided with the rainy season, and typically followed the direction of the creek.

Most of the painted bulbils that were placed in the creek were not recaptured. Only 19 (11 %) of the 180 painted bulbils placed in the creek were recovered, and these were near stand A. The creek bed near stand A was rocky allowing easier recovery of bulbils whereas the creek beds near B and C were sandy leading to burial and loss of bulbils. Thus, bulbil dispersal distance was only recorded at stand A. Nineteen bulbils were found with dispersal distances ranging from 8.6 to 206.2 m. The largest recorded distance (206.2 m) occurred in February, and other recorded distances occurred in April, May, September, October, and February (Fig. 4). Annual mean dispersal distance was 102 m ± 12.3. Even though long-distance dispersal of painted bulbils could not be measured near stands B and C, short distance dispersal was observed. Often when painted bulbils were placed in shallow moving water in stands B and C, they immediately rolled and bounced a short distance along the bottom of the creek. Mean bulbil movement of recovered bulbils for stand B was 0.6 m ± 0.1 and 0.3 m ± 0.04 for stand C. Disappearance of painted bulbils from caches along the banks mainly occurred at stands B and C. Only four bulbils disappeared from the banks near stand A, whereas 26 disappeared from the banks of stand B and 60 at stand C from January 2002–February 2003. These painted bulbils were not recovered following intensive searching in a radius of 5 m around the location where they were placed.

There was no correlation between the distances that tethered or painted bulbils moved and flow rate in any of the three stands (Spearman's Rank Correlations, $P > 0.05$). Mean flow rate among stands and the total number of bulbils recovered from traps, buckets, and drift lines were correlated (Spearman's $r = 0.56$, $P = 0.029$, $n = 15$), indicating high rates of bulbil dispersal during periods of high stream flow.

Discussion. BULBIL DISPERSAL. Even though bulbils of *Dioscorea oppositifolia* sink when placed in still water, our study shows that they are dispersed secondarily in moving water. Secondary bulbil redistribution by water thus overrides and extends the dispersal capacity of primary gravity dispersal (see also Hampe 2004). This finding has important implications for the invasiveness of this exotic plant and in preventing/minimizing further invasions.

Bulbils of *D. oppositifolia* are produced in late summer and detach from vines in early fall when water levels are low in the creek. Bulbils may get washed into the creek bed during rain, or they may fall into the creek directly off vines hanging over the top of the bank. In our study, the disappearance of painted bulbils from caches along the banks indicated that they may disperse into the creek from the floodplain. Alternatively animals may have removed some bulbils. There are no reports of animal dispersal of this species although Beyerl (2001) observed some small mammal herbivory of bulbils. Bulbils found in debris collected from the aluminum traps, bulbils captured in bucket traps, and the movement of painted and tethered bulbils downstream indicated that after their dispersal from the floodplain into the creek bed, bulbils are able to travel downstream. Bulbils are not buoyant in still water but move by saltation (Whitten and Brooks 1972) when placed in the shallow flowing water at Giant City State Park (Thomas, personal observation). Water currents roll bulbils forward and create lift allowing them to rise from the bottom of the creek bed. Once the forward momentum is lost, the bulbils settle to the bottom of the creek bed, and the cycle repeats (Whitten and Brooks 1972), allowing bulbils to disperse further downstream. Bulbil movement in deep rapid flowing water could not be observed because of lack of visibility, but depth and flow velocity of water have the greatest impacts on transportation of particles in water (Hewlett 1982). Since bulbils have been noted to disperse over 200 m after a major rainstorm event, it is likely that bulbils have increased momentum for lift with increased water depth and flow velocity.

Deposition of bulbils in debris on the aluminum traps, in bucket traps, and from drift lines on the banks probably was due to falling flow velocity following flood events. As large woody debris builds up, it creates a dam that redirects water flow, dissipates energy, and retains sediment, gravel, and organic matter (Marston 1982, Malanson 1993, Naiman and Decamps 1997). As energy dissipates, flow velocity decreases probably causing bulbils to settle in the debris or the traps. Also, as the creek overflows onto the floodplain, water flow velocity decreases causing deposition of sediments, litter (James 1985), and bulbils as well as diaspores of other invasive species. Indeed, diaspores of the invasive *Impatiens glandulifera* in central Europe have limited buoyancy but are dispersed along the bottom of streams and deposited on banks (Pyšek and Prach 1993). Diaspores of the invasive *Ampelopsis brevipedunculata* also disperse into creeks in natural areas of the northern Piedmont in Pennsylvania and are able to disperse several kilometers downstream (Robertson et al. 1994). Thus, water dispersal can be a common dispersal mechanism for invasion of new areas.

LIMITATION OF STUDY. Devising traps for measuring hydrochory is typically difficult in aquatic systems because of rapid currents and seasonal variation in water levels (Middleton 1995). During the course of this study, many traps were swept downstream and lost. The aluminum trap design was not ideal for hydrochory because the trapping surface was not horizontal to the water flow. Also most of the tethered and painted bulbils were never recaptured. Many of these bulbils could have been hidden under rocks and in crevices at stand A, buried in sand in stands B and C, moved downstream farther than the area searched, or removed by animals. Dispersal distances for *D. oppositifolia* via hydrochory in this study are minimum estimates; therefore, it is likely that bulbils may frequently be transported in excess of the 206 m measured. Even though there were complications with the hydrology and geology of the site, the results indicate clearly that bulbils of *D. oppositifolia* are able to disperse long distances in the watershed.

IMPLICATIONS. Bulbils of *D. oppositifolia* disperse secondarily in the stream at Giant City State Park. Bulbil dispersal by gravity is well timed during the season before water levels rise and flooding occurs. *Dioscorea oppositifolia* bulbils may remain viable for 12 months following dispersal (Thomas 2004). Other water dispersed diaspores spread during the same season in this forest system including *Taxodium distichum* and *Nyssa aquatica* (Middleton 2001; Schneider et al. 1988). To minimize invasion potential, bulbils of *D. oppositifolia* should be removed or prevented from entering the riparian corridor before winter when water levels are high.

Literature Cited

ASHTON, P. J. AND D. S. MITCHELL. 1989. Aquatic plants: patterns and modes of invasion, attributes of invading species and assessment of control programs, p. 111–147. *In* J. Drake, H. Mooney, F. Castri, R. Grove, K. Kruger, M. Rejmanek, and M. Williamson [eds.], Biological Invasions: a Global Perspective. Scope 37, Chap. 6. Wiley & Sons, Chichester, UK.

BAKER, H. G. 1965. Characteristics and modes of origin of weeds, p. 147–168. *In* H.G Baker, and G.L. Stebbins [eds.], The Genetics of Colonizing Species. Academic Press, London, UK.

BASINGER, M. 2001. Distribution of *Dioscorea oppositifolia* L. (Chinese yam) in Illinois. Illinois Department of Natural Resources Division of Natural Heritage, Springfield, IL.

BEYERL, T. 2001. Habitat and life history characteristics of *Dioscorea oppositifolia*, an invasive plant species in southern Illinois. M.S. thesis. Southern Illinois University, Carbondale, IL.

Boedeltje, G. 2004. Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. J. Ecol. 91: 786–796.

Boedeltje, G, J. P. Bakker, R. M. Bekker, J. M. Van Groenendael, and M. Soesbergen. 2003. Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. J. Ecol. 91: 855–866.

Brown, A. L. 1971. Ecology of Fresh Water. Heinemann Educational Books, London, UK.

Cooper, D. J., D. C. Anderson, and R. A. Chimner. 2003. Plant dispersal: Multiple pathways for woody plant establishment on floodplains at local to regional scales. J. Ecol. 91: 182–196.

Coursey, D. J. 1967. Yams: an Account of the Nature, Origins, Cultivation, and Utilization of the Useful Members of the Dioscoreaceae. Longmans, London, UK.

Cronk, Q., and J. Fuller. 2001. Plant Invaders: the Threat to Natural Ecosystems. Earthscan, Sterling, VA.

Darwin, C. R. 1855. Does sea-water kill seeds? pp. 255–258. *In* P.H. Barrett [ed.], The Collected Papers of Charles Darwin, Vol. 1, University of Chicago Press, Chicago, IL.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol. 88: 528–534.

DeBow, J. D. B. 1869. Chinese yam. Debow's Review, Agricultural, Commercial, Industrial Progress and Resources 6: 435–436.

Decamps, H., A. M. Planty-Tabacchi, and E. Tabacchi. 1995. Changes in the hydrological regime and invasions by plant species along riparian systems of the Adour River, France. Regulated Rivers Res. Manage. 11: 23–33.

DeFerrari, C. M., and R. J. Naiman. 1994. A multiscale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. J. Veg. Sci. 5: 247–258.

De Waal, L. C., L. E. Child, P. M. Wade, and J. H. Brock. 1994. Ecology and Management of Invasive Riverside Plants. John Wiley and Sons, Chichester, UK.

Drake, J. A., H. A. Mooney, F. Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson. 1989. Biological Invasions: A Global Perspective. John Wiley and Sons, Chichester, UK.

Forman, J., and R. V. Kesseli. 2003. Sexual reproduction in the invasive species *Fallopia japonica* (Polygonaceae). Amer. J. Bot. 90: 586–592.

Gillespie, R. N. 2003. Surveys for populations of *Dioscorea oppositifolia* L. (syn. *D. batatas* Decne.) within the Lusk Creek Watershed, Pope County, Illinois. Contractual Report, USDA Forest Service, Vienna Ranger District, Shawnee National Forest, IL.

Grabe, D. F. 1970. Tetrazolium testing handbook for agricultural seeds. Handbook on seed testing. Association of Official Seed Analysts, New Brunswick, NJ.

Gray, M. J., M. J. Crawley, and P. J. Edwards. 1987. Colonization, succession, and stability. Blackwell Scientific Publication, Oxford, UK.

Hampe, A. 2004. Extensive hydrochory uncouples spatiotemporal patterns of seedfall and seedling recruitment in a "bird-dispersed" riparian tree. J. Ecol. 92: 797–807.

Hawley, W. O. 1956. Dioscoreas as ornamental foliage plants. Natural Horticulture Magazine 35: 23–29.

Hewlett, J. D. 1982. Principles of Forest Hydrology. University of Georgia Press, Athens, GA.

Hierro, J. L., Maron, J. L., and R. M. Callaway. 2005. A biogeographic approach to plant invasions: the importance of studying exotics in their introduced and native range. J. Ecol. 93: 5–15.

James, C. S. 1985. Sediment transfer to overbank sections. J. Hydraulic Res. 23: 435–452.

Johansson, M. E., C. Nilsson, and E. Nilsson. 1996. Do rivers function as corridors for plant dispersal? J. Veg. Sci. 7: 593–598.

King, S. A., and R. T. Buckney. 2000. Urbanization and exotic plants in northern Sydney streams. Austral Ecol. 25: 455–461.

Kolb, A., P. Alpert, D. Enters, and C. Holzapfel. 2002. Patterns of invasion within a grassland community. J. Ecol. 90: 871–881.

Kollman, J., and D. Goetze. 1998. Notes on seed traps in terrestrial plant communities. Flora 193: 31–40.

Lancaster, R. 1989. Travels in China. A plantsman's paradise. Antique Collector's Club, Woodbridge.

Lippincott, C. H. 1909. Cinnamon vine. Floral Culture. January.

Lippincott, C. H. 1913. Hardy climbing vines. Floral Culture. January.

Malanson, G. P. 1993. Riparian Landscapes. Cambridge University Press, Cambridge, UK.

Marston, R. A. 1982. The geomorphic significance of log steps in forest streams. Ann. Assoc. Amer. Geog. 72: 99–108.

Middleton, B. A. 1995. Sampling devices for the measurement of seed rain and hydrochory in rivers. Bull. Torrey Bot. Club 122: 152–155.

Middleton, B. A. 2000. Hydrochory, seed banks, and regeneration dynamics across landscape boundaries in a forested wetland. Pl. Ecol. 146: 169–184.

Mohlenbrock, R. H. 1981. Giant City State Park: an Illustrated Handbook. State of Illinois, Department of Conservation, Springfield, IL.

Mohlenbrock, R. H. 1986. Guide to the Vascular Flora of Southern Illinois. Southern Illinois University Press, Carbondale, IL.

Naiman, R., and H. Decamps. 1997. The ecology of interfaces: riparian zones. Ann. Rev. Ecol. Syst. 28: 621–658.

Naiman, R., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecol Appl. 3: 209–212.

Okagami, N. and N. Tanno. 1991. Dormancy in *Dioscorea*: comparison of dormant characters in bulbils of a northern species (*D. opposita*) and a southern species (*D. bulbifera* var. *vera*). J. Pl. Phys. 138: 559–565.

Ozinga, W. A., R. M. Bekker, J. H. J. Schaminée, and J. M. Van Groenendael. 2004. Dispersal potential in plant communities depends on environmental conditions. J. Ecol. 92: 767–777.

PARENDES, L. A. AND J. A. JONES. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews Experimental Forest, Oregon. Cons. Biol. 14: 64–75.

PYŠEK, P. AND K. PRACH. 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. J. Biogeog. 20: 413–420.

PYŠEK, P. AND K. PRACH. 1994. How important are rivers for supporting plant invasions? p. 19–26. *In* L.C. de Waal, L.E. Child, P.M. Wade, and J.H. Brock [eds.], Ecology and Management of Invasive Riverside Plants John Wiley & Sons, Chichester, UK.

ROBERTSON, D. J., M. C. ROBERTSON, AND T. TAGUE. 1994. Colonization dynamics of four exotic plants in a northern Piedmont natural area. Bull. Torrey Bot. Club 121: 107–118.

SAUER, J. D. 1988. Plant Migration. University of California Press, Berkeley, CA.

SCHNEIDER, R. L. AND R. R. SHARITZ. 1988. Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. Ecology 69: 1055–1063.

THEBAUD, C. AND M. DEBUSSCHE. 1991. Rapid invasion of *Fraxinus ornus* L. along the Herault River system in southern France: the importance of seed dispersal by water. J. Biogeog. 18: 7–12.

THOMAS, J. R. 2004. Dispersal of the exotic invasive *Dioscorea oppositifolia* L. along a tributary of Drury Creek in Giant City State Park, southern Illinois. M.S. thesis. Southern Illinois University, Carbondale, IL.

THOMAS, J. R., B. A. MIDDLETON, AND D. J. GIBSON, in press. A landscape perspective of the invasion of the exotic Chinese yam in a pristine watershed. Biol. Invasions.

THOMPSON, K., J. G. HODGSON, J. P. GRIME, AND M. J. W. BURKE. 2001. Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. J. Ecol. 89: 1054–1060.

TU, M. 2002. Element Stewardship Abstract for *Dioscorea oppositifolia* L. syn. *Dioscorea batatas* Decn. [Online]. Available: http://tncweeds.ucdavis.edu/esadocs/documnts/diosopp.html. The Nature Conservancy, Arlington, VA.

USDA, NATIONAL RESOURCE CONSERVATION SERVICE 2003. The PLANTS database. [Online]. Available: http://plants.usda.gov/plants. National Plant Data Center, Baton Rouge, L.A.

VELLEND, M., J. A. MEYERS, S. GARDESCU, AND P. L. MARKS. 2003. Dispersal of *Trillium* seeds by deer: implications for long distance migration of forest herbs. Ecology 84: 1067–1072.

VILA, M. AND P. LLORET. 2000. Seed dynamics of the mast seeding tussock grass *Ampelodesmos mauritanica* in Mediterranean shrublands. J. Ecol. 88: 479–491.

WHITTEN, D. G. A. AND J. R. V. BROOKS. 1972. The Penguin Dictionary of Geology. Penguin Books, Harmondsworth, Middlesex, England.

YATSKIEVYCH, G. 1999. Steyermaark's flora of Missouri. Missouri Department of Conservation, Jefferson City, Missouri, in cooperation with the Missouri Botanical Garden, St. Louis, MO.