SOUTHERN ILLINOIS UNIVERSITY
Carbondale

Southern Illinois University at Carbondale
Carbondale Illinois 62901

Department of Plant Biology
Mail Stop 6509

(618) 453-3231 fax: (618) 453-3441
e-mail: dgibson@plant.siu.edu

David J. Gibson
Professor of Plant Biology

02 November 2001

Jody Shimp
Illinois Department of Natural Resources
State Highway 37
Benton, IL 62812

RE: Wildlife Preservation Fund Grant #01-021W
Habitat and reproduction of *Dioscorea batas* an invasive plant species in southern Illinois.

Dear Jody,

As per our telephone discussion today I enclose a copy of Tammie Beyerl's MS thesis. This thesis constitutes the SIUC final commitment for the Wildlife Preservation Fund Grant that we were awarded. You indicated to me that you would forward copies of this thesis to Bill McClain in Springfield on our behalf.

Thank you for your assistance with this and our other collaborative projects.

Yours sincerely,

David Gibson Professor of Plant Biology

cc. Sonjie Schwartz (SIUC ORDA)

HABITAT AND LIFE HISTORY CHARACTERISTICS OF *DIOSCOREA OPPOSITIFOLIA*, AN INVASIVE PLANT SPECIES IN SOUTHERN ILLINOIS.

By

Tammie Beyerl

B.A. in Plant Biology
Southern Illinois University
at Carbondale
1999

A Thesis
Submitted in Partial Fulfillment of the Requirements
for the Master of Science Degree

Department of Plant Biology
in the Graduate School
Southern Illinois University
At Carbondale

October 2001

AN ABSTRACT OF THE THESIS OF

TAMMIE BEYERL, for the Master of Science Degree in Plant Biology, presented on September 21, 2001 at Southern Illinois University at Carbondale.

TITLE: Habitat and life history characteristics of *Dioscorea oppositifolia*, an invasive plant species in southern Illinois.

MAJOR PROFESSOR: Dr. David J. Gibson

Dioscorea oppositifolia is an invasive plant species that is an increasing problem in Natural Areas in southern Illinois. This species has the potential to spread rapidly through the production of axillary tubers (modified stems) called bulbils or tubercles. Each vine can produce numerous bulbils and each bulbil has the potential to produce a new plant. Very little is known about the ecology of this species as an escaped exotic. A study was conducted to quantify and qualify the habitat of *D. oppositifolia* in southern Illinois and to determine some of its life history characteristics. The most common habitat was at the edges of rich, moist forests, drainageways, and streambanks in silty loam soils. The natural communities that the species was most commonly found in were mesic-upland forests, mesic floodplain forests, and developed land. Subpopulations of *Dioscorea oppositifolia* exhibited one of two types of stage structure. Type I subpopulations, which were composed mostly of short, single leafed individuals, had a low frequency of bulbil producing individuals and very few flowering individuals. Type II subpopulations were composed mostly of longer vines that produced numerous bulbils and had a greater number of flowering individuals. Vines of Type I subpopulations produced a mean of 8.97 = SE 2.38 bulbils per meter of stem, mean vine length was 83.23 cm = SE 13.59 cm and their mean tuber biomass was 1.13 g = SE0.33. Vines in Type II subpopulations produced a mean of 33.42 = SE 3.17 bulbils per meter of stem and had a mean tuber biomass of 4.00 g = SE 0.62.

A plant species richness survey was conducted and it was determined that species richness was significantly higher (t = -5.07, DF = 76.8, p = .0001) in plots without *D. oppositifolia* (mean number of species = 6.9 ± SE 1.6) than in plots with *D. oppositifolia* (mean number of species = 4.6 ± SE 2.7). Both the number of native plant species and the percent cover of native species was significantly lower in plots with *D. oppositifolia.* This study suggests that *D. oppositifolia* is a serious threat to native plant species richness and abundance and that it threatens some of the most pristine habitats in southern Illinois.

ACKNOWLEDGEMENTS

Many thanks to my major professor, Dr. David Gibson, for his advice and guidance and for the privilege of learning ecology under his tutelage. Thanks also to Dr. Philip Robertson and Dr. Raymond Stotler for serving on my committee and imparting their experience and knowledge to improve my research and writing. A special note of gratitude to Dr. Walter Sundberg and Dr. Donald Tindall for all of their encouragement in getting me to attend graduate school.

I am truly grateful to Mark Basinger and Jody Shimp for introducing me to the species *Dioscorea oppositifolia* and for encouraging me to study it and for sharing their knowledge of the species. My sincere gratitude to the Illinois Department of Natural Resources for funding of this research through the Natural Heritage Small Project Fund. Thanks also to Andy West at the Trail of Tears State Forest for initiating the herbicide study and sending me the treated and untreated bulbils.

Thank you to my friends and colleagues in the Department of Plant Biology for help in various aspects of my research and/or analyses and writing: Shibi Chandy, Joe Ely, and Yuki Kobiyama.

My greatest debt of gratitude is to my wonderful husband, Richard, for his unwavering support and encouragement. He pushed me to go to college soon after we were married and he gave me the confidence to get through even the most difficult times. He made many sacrifices so that I could succeed and he even braved poison ivy and blackberry brambles to help me in the field. I cannot imagine having accomplished this without him.

TABLE OF CONTENTS

INTRODUCTION

Exotic plant species are consistently introduced into the United States for such purposes as ornamental landscaping, agriculture, and soil conservation (Devine 1998). Invasive plants are those exotic species which are new to the region, spread beyond their planted boundaries, persist without human intervention, and have serious impacts on their new environment (Simberloff *et al.* 1997, Davis and Thompson 2000). There have been numerous studies that describe the impacts of invasive plant species on native vegetation (eg. Melgoza *et al.* 1990, Myster and Pickett 1992, Dillenberg *et al.* 1993, Woods 1993, Gould and Gorchov 1999, Schultz and Thelen 2000). These impacts include alteration of hydrological patterns, fire cycles, and soil chemistry, reduction of nutrient, water, and light availability and reduction of biodiversity (Coblentz 1990, Schmitz and Brown 1994, Vitousek *et al.* 1996, Simberloff et al. 1997, Gordon 1998). The effects of invasive plant species are estimated to cost U.S. taxpayers billions of dollars every year (Lockhart *et al.* 1999, National Biological Information Infrastructure 2000).

Dioscorea oppositifolia L. is an exotic species that has recently raised serious concern among southern Illinois land managers and biologists as it has become more and more abundant in local Natural Areas. It is believed that this species could pose a serious threat to native plant species because of its dense growth form and prolific vegetative reproduction. *Dioscorea oppositifolia* is a twining vine that climbs adjacent vegetation forming a thick blanket of leaves that presumably shades other species from the sun and is heavy enough to bend and break the stems of herbaceous plants and small trees. *Dioscorea oppositifolia* seems to be spreading very rapidly through production of axillary tubers (bulbils) which function as vegetative propagules. There is very little knowledge to date of the ecology and potential invasivness of this species in southern Illinois. Previous to the following research, there had been no studies describing the habitat of *D. oppositifolia* and its life history characteristics outside of cultivation were virtually unknown. There had been no research on the impacts of this species to ecosystems it has invaded in the region. The purpose of this study was to gather information on the habitat and life history characteristics of *D. oppositifolia* and to begin to assess its effects on native vegetation.

RESEARCH OBJECTIVES AND HYPOTHESES

The first research objective was to characterize the habitat of *D. oppositifolia* in southern Illinois. In Missouri, this species is described as occurring along roadsides and at old homesites as well as in mesic bottomland forests (Yatskievych 1999). Local land managers also reported finding the species near streams, along roadsides, and at old homesites in southern Illinois (Basinger, Shimp, pers. comm.) and Mohlenbrock (1986) describes it as being adventive in disturbed areas of Jackson County. The goal of this study was to determine what environmental characteristics (light intensity, soil moisture, soil pH, distance to stream, slope, and aspect) and species associations correspond to the presence of *D. oppositifolia* in southern Illinois. The first null hypothesis was that environmental characteristics and species associations would not be correlated among sites with *D. oppositifolia*.

The second research objective was to determine whether *D. oppositifolia* is eliminating native plant species from plots where it occurs. Since *D. oppositifolia* has already invaded high quality Natural Areas such as Lusk Creek, this objective was needed to help in the assessment of the species potential threat to native ecosystems and to threatened and endangered species. The second null hypothesis was that there would be no difference in species richness and abundance between plots with *D. oppositifolia* and those without it.

A third research objective was to describe some of the life history characteristics of *D. oppositifolia* to achieve a better understanding of the role of vegetative reproduction of this species. This study examined the importance of both the underground tubers and the bulbils relative to growth and fecundity. The study also strove to conclude whether or not this species is reproducing sexually in southern Illinois since it was reported to flower but not produce fruit in its current U.S. range. Knowledge of the species' life history was needed for the assessment of its potential to spread and to help in the development of control methods. The third null hypothesis was that there would be no difference in vigor between plants grown from underground tubers and plants grown from bulbils.

LITERATURE REVIEW

Invasives

Exotic species (also called alien, introduced or non-native species) are those found outside of their natural range (Devine 1998). Exotic plant species are introduced into the United States in many ways. They may be brought in intentionally as ornamental garden plants, agricultural crops, or to aid in soil conservation (Baker 1986). They may arrive accidentally mixed in shipments of lawn or pasture seed, for example (Devine 1998). Although plants do spread naturally beyond their native ranges (eg. by migratory birds carrying seeds far distances), this occurs only rarely. Human intervention is responsible for the introduction of most exotic species and human disturbance is almost always necessary for a successful invasion by an exotic because most cannot invade closed vegetation (Baker 1986, Silvertown and Lovett Doust 1993). Researchers estimate that a new species arrived in the Hawaiian Islands once every 70,000 years prior to human intervention. Today, a new exotic becomes established in the islands every 18 days (Devine 1998). Exotic species which spread into areas where they were not planted, persist without human assistance, and displace native species are called invasives (Simberloff et. al. 1997). Davis and Thompson (2000) have devised a classification scheme to rate colonizing plants based on three criteria: dispersal distance, origin, and impact on the environment. According to this classification scheme, a colonizer should be called invasive only if it is novel to the region being colonized and has a great impact on the new environment. The dispersal distance may be short or long. It is inherent in these definitions of the term "invasive" that these are exotic species and it is therefore redundant to use the terms exotic, alien, introduced, non-native, or non-indigenous to modify the term invasive species.

Invasive plants can cause serious disruptions to natural ecosystems by displacing native plants and reducing biodiversity (Coblentz 1990, Vitousek *et al.* 1996, Simberloff et. al. 1997). Aggressive invaders can reduce the amount of light, nutrients, water, and space available for native species, and alter hydrological patterns, soil chemistry, and fire cycles (Vitousek *et al.* 1996). These changes can result in loss of threatened and endangered species, loss of habitat and or food sources for wildlife, and disruption of native plant-animal associations such as pollination, seed dispersal and host plant relationships (Vitousek *et al.* 1996, PCA 2000). Exotic species have contributed to the decline of 42% of the 958 species listed as threatened or endangered in the U.S. and are the major influence for the decline of 18 % of those species (The Nature Conservancy 2000). The National Biological Information Infrastructure (NBII 2000) reports that invasive plants cost the U.S. economy an estimated $123 billion annually. Experts estimate that invasive plants already infest over 40 million ha and another 1.2 million ha become dominated by invasive plants each year (NBII 2000).

Sixty-one percent of U.S. National Park supervisors polled in 1996 reported invasive plants as moderate to major problems in the parks (The Nature Conservancy 2000). In a recent survey of The Nature Conservancy's land stewards, 60% reported invasive plants as one of their top management problems while 12% reported invasive plants as their single most serious problem. These stewards reported that there are at least 237 invasive plant species on their preserves and that these plants are threatening the ecological balance of the preserves (The Nature Conservancy 2000).

It is very difficult to predict a species potential for invasiveness. Williamson's Tens Rule states that only 10% of exotic species survive introduction to a new region and that only 10% of those that survive will become invasive (Williamson 1996). Table 1 presents some of the characteristics that are common to invaders as listed by various authors who study invasives (Baker 1965, Bazzaz 1986, Simberloff et. al.1997). Very few invasives possess all or even most of these characteristics, however, and possession of these characteristics does not necessarily mean a plant will become invasive (Groves and Burdon 1986). Many other factors contribute to the likelihood of an exotic species becoming invasive in a new environment. These include the health of the ecosystem it is introduced into, similarity of the introduced climate to its original climate, whether or not its natural predators are present, whether or not its pollinator is present, disturbance regime of the new environment, and the competitive abilities of the species present in the new environment (Devine 1998, Lonsdale 1999).

Table 1. Some of the characteristics common to invaders (compiled from: Baker 1965, Bazzaz 1986, and Simberloff et. al. 1997).

1. broad-niched
2. self or wind pollination or non specialized pollinators
3. rapid growth to reproductive maturity
4. high allocation of resources to reproduction
5. short life cycle
6. resistance or opportunistic response to disturbance
7. ability to spread rapidly
8. prolific vegetative reproduction
9. an ability to out compete natives
10. rapid response to resource availability

A fluctuating resources model developed by Davis *et al.* (2000) theorizes that a plant community becomes more invasible as the amount of resources available increases either because of decreased use of resources by the current vegetation or because of an increased supply of resources. Decreased use of resources can occur whenever the number of plants in the community is reduced such as in the case of disturbance, herbivory or disease. For example, an increase in resource supply can result when rainfall exceeds average rainfall or when fertilizer is applied.

Many ecologists consider invasive species to be one of the most severe environmental problems worldwide (Devine 1998, NBII 2000). Invasion by exotic species is the second leading threat to biodiversity behind loss of habitat and it is a major cause of habitat loss (Devine 1998, NBII 2000). Although invasive species are a major environmental problem, the magnitude of this problem has only recently begun to be appreciated. Much research is needed to better understand the ecology of invasions and to develop our ability to assess a species potential for invasion. This would allow us to develop control methods for species with invasive potential that are just getting established instead of waiting until they have already become serious ecological problems.

Invasives in Illinois

The Illinois Department of Energy and Natural Resources (IDENR 1994) reports that the invasion of exotic species is one of the most serious threats to Illinois forests and that the problem of invasive species is becoming more severe. Forests contain over half the native flora and over half of the endangered plant species in the state (IDENR 1994). These forests also provide 75% of the state's wildlife habitat (IDENR 1994).

As of 1994, Illinois had 782 exotic plant species that had escaped cultivation and become naturalized, this constitutes 27.5 % of the state's total flora (Rejmanek and Randall 1994). Of these, 78% were introduced from outside of North America (IDENR 1994). One-fifth of the Illinois flora can be classified as invasive exotic plants. These invasive exotic plants can alter the structure of ecosystems and decrease biodiversity (IDENR 1994). The rate of introduction has increased in recent years and the number of exotics that have become invasive continues to increase (Henry and Scott 1981, IDENR 1994).

The damage to ecosystems and ecological costs to the state caused by invasive plants prompted passage of the Illinois Exotic Weed Act (IEWA) in 1991 (IDENR 1994). This law makes it illegal to buy, sell, distribute or plant seeds, plants, or plant parts of those species recognized as "exotic weeds" (IDENR 1994). The IEWA defines exotic weeds as "those plants not native to North America which, when planted, either spread vegetatively or naturalize and degrade natural communities, reduce the value of fish and wildlife and wildlife habitat, or threaten an Illinois endangered species". There are numerous species that fit this definition but there were only 3 exotic plant species (*Lonicera japonica, Rosa multiflora,* and *Lythrum salicaria*) listed by the IEWA by 1994.

Dioscorea

Dioscorea is the largest genus of the Dioscoreaceae (yam family) with over 600 species of tropical, subtropical and/or warm temperate climates. All members of the genus originated either in China, Africa, or Central/South America but had spread worldwide by the end of the Cretaceous period (Coursey 1967). The plants have annual, twining stems which develop from tubers that resprout year after year. They are dioecious and the fruits are dry capsules (Coursey 1967). The leaves are simple and entire with a broad blade, usually having a cordate base. Venation is reticulate: parallel and arcuate main veins with a network of lateral veinlets (Zomlefer 1994). The petioles are usually long with a pulvinus at both ends often with a stipule-like flange on the basal pulvinus (Zomlefer 1994). Members of this genus typically contain alkaloids and have extrafloral nectaries. Many species are cultivated for their starchy tubers and others are cultivated for the manufacture of steroidal hormones used as oral contraceptives. Many species produce commercial quantities of Diosgenin a precursor of progesterone and cortisone (Mabberly 1989).

There are two species of Dioscorea native to Illinois: *D. quarternata* Walt. and *D. villosa* L. Both have ovate, acuminate, cordate leaves. The leaves of *D. quarternata* are 5-12 cm long and 4-10 cm wide and may be alternate or opposite with the lowest set whorled, the capsule has three wings and is 2.5-3 cm long. *D. quarternata* is restricted to the southern 1/3 of the state. The leaves of *D. villosa* are 5-10 cm long, 3-8 cm wide, alternate, lowest set pseudo-whorled, capsule has three wings and is 1.5-2.5 cm long. *D. villosa* is distributed over the whole state. Neither of these species produce axillary tubers (Mohlenbrock 1986).

Dioscorea oppositifolia L.

Dioscorea oppositifolia L (syn. *D. opposita* Thunb., *D. batatas* Decne., *D. divaricata* Blanco) is an invasive, non-native vine that has the potential to spread rapidly through the production of axillary tubers called bulbils (Plants for a Future 1999). These bulbils are modified stems that have the ability to produce new individuals (Mabberly 1989, Zomlefer 1994). *D. oppositifolia* has a persistent underground root-like tuber that resprouts annually. These cylindrical tubers can grow to 1m long and are vertically oriented into the ground (Coursey 1967). The stems are round climbing vines that twine in a dextrorse manner (from the left to the right) (Coursey 1967, Zomlefer 1994). The leaves are usually arranged oppositely but alternate leaf arrangement is also common, especially in the upper nodes. Leaves may also be ternate (in whorls of 3) although this arrangement is less common than the others mentioned (Yatskievych 1999, personal observation). The leaf shape is variable with the first leaves produced being ovate and the leaves of the upper nodes being ovate, hastate, or sagittate (personal observation). In all cases, the leaves have a deeply lobed cordate base and an accuminate tip (Gleason and Cronquist 1991, Yatskievych 1999). This species often has reddish-purple coloration along the leaf margins, petioles, and stems (personal observation). The small, white flowers are produced in panicles and have a cinnamon fragrance. The fruit, a capsule, is broader than long and the seeds are completely encircled by a wing (Plants for a Future 1999). This species is more frost tolerant than many of the Dioscoreas and thus its climatic range extends from tropical to northern temperate.

Both the tuber and the bulbils are edible though the bulbils are generally not used as food. The tuber is also used as an herbal tonic. The Plants for a Future web site lists numerous medicinal uses for the tubers (Table 2). The tubers contain allantoin, which, according to PFAF, speeds the healing process. They also contain starch, mucilage, amylase, amino acids, and glutamine (PFAF 2000). The species use as an herbal and its attractive appearance along with its ease of propagation make it popular for cultivation.

Table 2. Ailments treated with *D. oppsositifolia* tubers (Plants for a Future 2000).

1. Asthma, dry coughs
2. Hyperthyroidism
3. Weight loss, poor appetite
4. Poor digestion, chronic diarrhea
5. Frequent or uncontrollable urination
6. Tiredness
7. Diabetes
8. Emotional instability
9. Ulcers, boils, abscesses, snakebites and scorpion stings (leaf juice)

In 1970, this species had not yet escaped cultivation but was growing wild in disturbed areas of Jackson county by 1986 (Mohlenbrock 1970, 1986). Basinger (2001) found escaped populations of *D. oppsositifolia* in 13 counties in southern Illinois and the species has been reported in eight more counties. Jody Shimp of the Illinois Department of Natural Resources (pers. comm.) reports that this species is repeatedly mentioned by farmers and range managers as a serious weed problem in southern Illinois. According to Yatskievych (1999), this species can eliminate native understory plants due to its dense growth.

Dioscorea oppositifolia is native to China and was introduced in the U.S. as an ornamental vine (Coursey 1967, Yatskievych 1999). Hawley (1956) reports that the species *D. divaricata*, which is thought to be the same species as *D.*

oppositifolia, was introduced to the U.S. mainland from Hawaii in 1913 as an ornamental foliage plant. Today, it is distributed in 23 states in the U.S. from Georgia north to Vermont and west to Kansas and Oklahoma (see Fig. 1: USDA 2001). The species is most common in the southeastern US and is most abundant in Kentucky, Tennessee, the Carolinas, and Georgia (Basinger 2001). Although this species is an increasing problem as an invasive, no studies had been done on it in southern Illinois previous to this study. No information existed on its ecology and reproduction and its distribution and demography had not been recorded. It is necessary to learn more about this plant in order to determine its potential for invasion, the extent of its spread, and predict what habitats it may be found in. Gathering knowledge of this species can help in assessing its potential invasiveness and planning control methods to try and prevent it from destroying native ecosystems.

MATERIALS AND METHODS

Study Area

There were six sites in four counties in southern Illinois used for this study (Table 3). All of the *Dioscorea oppositifolia* plants at a given site were considered as one population. Within each site, there was microsite level variation in environmental features, for example, some of the sites were roadsides that had *D. oppositifolia* growing on either side of the road and each side of the road had different slope, aspect, soil moisture, etc. so the *D. oppositifolia* plants growing on different sides of the road were considered as separate subpopulations. Within the six sites, there were 11 subpopulations of *D. oppositifolia* that were investigated for one or more aspects of this research.

Table 3. Location and habitat of study sites.

Site	County	Township & Range	Habitat
Douglas Dr.	Jackson	T9S R1W section 28	Mesic upland forest
Thompson Woods	Jackson	T9S R1W sections 28 & 29	Mesic upland forest
Landreth Rd.	Jackson	T10S R2W section 34	Mesic upland/Cultural
York Lane	Gallatin	T10S R8E section 36	Dry-mesic upland
Lamb Rd.	Hardin	T11S R10E sections 29 & 32	Mesic floodplain
Lusk Creek	Pope	T11S R6E section 34	Mesic floodplain

The Douglas Dr. and Thompson Woods sites are both located on the Southern Illinois University Carbondale campus. Thompson Woods is 4.05 ha, oak-hickory remnant that was described as wilderness as late as 1948 (Halvey

1979). Thompson Woods was purchased by Southern Illinois University in 1939 (Halvey 1979). The predominate soil types in the vicinity are Hosmer associations formed in loess or loess and loamy material (Herman 1979). Two subpopulations within Thompson Woods were used in this study (TWI and TWII). Both subpopulations are at the southern end of the woods adjacent to paved footpaths and extending into the woods (all plants sampled were within the woods and not against the paths). The subpopulations are approximately 50 m apart and there is a shallow ditch between them. The Douglas Dr. site also consists of two subpopulations, Douglas Dr. I (DDI) is along the mowed right-of-way parallel to the paved road and Douglas Dr. II (DDII) is within the adjacent forest. The predominant soil type in the immediate vicinity of these subpopulations is Stoy silt loam (Herman 1979). This is a poorly drained, 2-4 % sloping soil of rolling ridgetops, drainageway side slopes, and footslopes (Herman 1979).

Landreth Rd. is a gravel road that begins at the Jackson-Union county line off of State Highway 127. The surrounding area has a number of peach and apple orchards. The soil in the area consists mostly of Hosmer silty clay loam with 12 to 18 % slopes and severely eroded (Herman 1979). This is a moderately well drained soil along drainageways and hillsides (Herman 1979). This population was divided into three subpopulations for this study. The Landreth Rd. I (LRI) subpopulation is along the south side of the road near the remains of an old homesite. Landreth Rd. II (LRII) is along the north side of the road in and along the roadside drainage ditch and climbing up a bank that borders the road. The third subpopulation Landreth Rd. IIA (LR IIA) is also climbing the bank on the north side of the road but is further northeast in a population of *Rhus glabra*. At the top of the bank is a current homesite.

York Lane is a gravel road off of Pound's Hollow Rd. in an area that is used primarily for recreational activities such as hunting and hiking. The typical soil of the immediate area is Hosmer silt loam with 1-4 % slopes on ridgetops and slope breaks and Hosmer silt loam with 4-7 % slopes on ridges and other gentle slopes (Wallace and Fehrenbacher 1967). These soils are moderately well-drained, have a fragipan and formed in silty material or loess (Wallace and Fehrenbacher 1967). This population was divided into two subpopulations for this study. York Lane I (YLI) is a scattered population growing along the north-northeast side of the road and the roadside drainage ditch for over 200 m. York IIA (YLIIA) is an extremely large, dense population growing at an old homesite on the south side of the road and extending into the woods.

The Lusk Creek population is within the Lusk Creek Natural Area scattered along the streambed and stream bank and extending into the surrounding forest. This area is characterized by Muskingum and Berks soils on steep hillsides (30-60 % slopes) (Parks 1975). These are well-drained soils that are moderately deep to bedrock and are formed from silty or loamy material with some sandstone flagstones (Parks 1975).

The Lamb Rd. population is along a bank between the paved road and a streambed below and extending into the floodplain forest. There is an old church building on the site and there is an area of the site that was recently logged. The *D. oppositifolia* population is on the southeast side of the road and extends for approximately 50 m. The predominant soil types in the immediate area are Wakeland silt loam, a deep, nearly level, poorly drained soil formed in silty sediment and Wellston-Berks complexes which are deep, well-drained soils with 12-18 % slopes (Parks 1975).

Habitat Characterization

In order to characterize the habitat of this species, a floristic survey was made at the six sites listed in Table 3. Light intensity was measured monthly May-August at Landreth I and II, TW I and II, and Douglas I and II using a Li-Cor® LI-191SA Line Quantum Sensor (Li-Cor Environmental, Lincoln, NE). This instrument measures photosynthetic photon flux density (PPFD). A standard reading of PPFD was taken outside of each plot, in full sun, and then readings were taken inside the plots. The PPFD values from inside the plots were divided by the standard readings so that light intensity is expressed as a proportion of full light. Soil moisture was measured twice monthly May-August using a Kelway® soil acidity and moisture tester model HB-2 (Kel Intruments Co., Inc., Wyckoff, NJ) at the same sites as for light intensity. Ten soil core samples were collected from within each of the 11 subpopulations used in this study and sent for analysis of total nitrogen content (organic and inorganic) and particle size (hydrometer method) to A & L Analytical Laboratories, Inc, Memphis, TN.

Percent slope and aspect were determined by entering the subpopulations of *Dioscorea oppositifolia* into Arcview® Geographical Information System (GIS), as points on quadrangle maps obtained from the USGS Data Clearinghouse and overlaying the corresponding digital elevation models.

Analysis of habitat characteristics was done using ordinations on matrices of sample plots by associated species cover. Detrended Correspondence Analysis was performed using PC-ORD (Version 4, McCune and Mefford 1999) to see if the abundance of *D. oppositifolia* was related to eigenvalues derived from cover of plant associates. The ordination analysis was done by excluding *D. oppositifolia* and species that occurred in less than two plots from the matrix. Three plots that were extreme outliers were also removed from the matrix.

Natural community classification follows White and Madany 1978. Nomenclature is according to Gleason and Cronquist (1991) except for the name *Dioscorea oppositifolia* L., which is according to Yatskievych (1999). The synonym *Dioscorea batatas* Decne. has been the more commonly used name for this species in the past, however, the name applied by Linnaeus has priority. These species are listed as synonyms by Kartesz (1994) and Yatskievych (1999). The means for all analyses are reported as means ± standard error (SE).

Species Richness and Abundance

To determine if *Dioscorea oppositifolia* is eliminating native species, quadrats were set up in pairs. Eight $1m^2$ quadrats were set up within subpopulations of *D. oppositifolia* at each of five sites (York Ln., Landreth Rd., Douglas Dr., Thompson Woods, and Lusk Creek). For each of these quadrats in the Douglas Dr., Lusk Creek, and Thompson Woods populations, another quadrat was set up at a random angle by choosing a random number between one and 360 from a random number table (Zar 1996, Table B.41) and placing an adjacent quadrat two meters outside of the *D. oppositifolia* cluster in this direction. At the

Landreth Rd., York Ln, and Douglas Dr. sites, which are linear populations running along roadsides, quadrats without *D. oppositifolia* were set up adjacent to those with *D. oppositifolia* to create paired samples. The number of species present in each quadrat was counted and percent canopy cover of each species was visually estimated using a modified Daubenmire scale (Abrams and Hulbert 1987). The density of *D. oppositifolia* was determined in each of the quadrats in which it occurred.

Paired sample t-tests were used to analyze species richness and abundance data to determine if the presence of *D. oppositifolia* was related to the richness and abundance of native plant species. The independent variables for these paired samples were data from quadrats with *D. oppositifolia* and from adjacent quadrats without *D. oppositifolia*. The dependent variables were the number of species and percent cover of species occurring at > 25% frequency in the plots. The means for all analyses are reported as means ± standard error (SE).

Life History Characterisics

The growth, bulbil production, and fruit/seed production of *Dioscorea oppositifolia* was examined as part of the life history study. Ten plants each were randomly selected from the DDI and II, TWI and II, and the LRI and II subpopulations. A numbered metal tag was tied around the base of the stem of each plant so that it could be identified for monitoring throughout the growing season. The stem length from the ground to the end of the dominant (longest) stem was measured on six occasions, April 22 - 24, May 10-12, June 1-2, June 29 through July 2, July 26-28, and August 22-25. The number of bulbils produced per meter of stem was counted for each plant at the time the plants were harvested (August 22-25). None of the tagged individuals flowered but there were a few plants that did flower in each subpopulation except for LRI. LRII had the greatest number of flowering individuals of the six subpopulations monitored but none of the flowers developed into fruits. Dried inflorescences were collected and examined under a dissecting scope to determine their sex.

At the end of the growing season, the plants were dug up, cleaned, and dried at 80° C for 48 hours. The total biomass (g dw) was measured for each plant and the shoots, roots (secondary), tubers (primary root), and bulbils separately.

One-way ANOVA was used to analyze data from the life history field study. The independent variable was site (six levels), and the dependent variables tested in separate ANOVAs were stem length, relative growth rate measured from stem length (RGR_h), number of bulbils produced per meter of stem, and dry weight of individual plant parts. A Dunn-Sidak adjustment $(1-(1-\alpha)^{1/k})$ of the alpha level had no effect on the outcome of the ANOVA tests. Repeated measures ANOVA was performed using the General Linear Model procedure in SAS version 8 (1999) for RGR_h and stem length. RGR_h was calculated as

$$\mathrm{RGR} = \frac{\log_e M_2 - \log_e M_1}{T_2 - T_1}$$

where M_1 and M_2 were the total vine length at the beginning (T_1) and the end (T_2) of the period, respectively. Plant height (stem length) was measured 6 times (1, 21, 42, 68, 93, and 121 days into the study). There were 5 levels for RGR_h (21, 42, 68, 93, and 121 days) thus requiring a repeated measures ANOVA for the variables stem length and RGR_h.

Analysis of variance on ranks was used for the dependent variables of shoot (leaf and stem) and tuber dry weight and for the number of leaves and number of bulbils produced among 6 subpopulations. This nonparametric method was used because the data exhibited extreme non-normality that was not corrected through transformations. These analyses were performed using the NPAR1WAY procedure in SAS version 8 (1999). The means for all analyses are reported as means ± standard error (SE).

During the study, it became apparent that different subpopulations exhibit different stage structure. This stage structure was classified into two types: Type I subpopulations - the single-leafed, non-reproductive stage structure that consisted of relatively few bulbil producing vines, many single-leafed individuals under 20 cm tall and in which flowering was rare and Type II subpopulation – the reproductive vine stage structure that consisted mostly of longer vines that produced bulbils and had a greater number of flowering individuals. Type II populations formed dense monocultures that blanketed adjacent vegetation. Per chance, the six subpopulations that were selected for monitoring target individuals were all Type I subpopulations. In order to compare these populations with Type II populations, 25 tubers each were randomly collected at the end of the growing season, from York Lane IIA (YLIIA) and Landreth Rd. IIA (LRIIA) which are both Type II subpopulations. The mean biomass (g dw) of these tubers was then compared with that of the tubers from the 57 plants that were monitored throughout the 2000 growing season from the six Type I subpopulations (DDI and II, TWI and II, and LRI and II). The tubers from the six Type I subpopualtions were combined in pairs according to study site to create three larger groups (LR, TW, and DD).

Ten vine segments with bulbils attached were also collected from each of these Type II subpopulations in order to compare the number of bulbils produced per meter of stem between the two types. One-way ANOVA was used to test for differences in tuber biomass (g dw) and number of bulbils produced per meter of stem among the five subpopulations.

Bulbil survivorship was also examined as part of the life history study. The length and width was measured and the number of eyes was counted for 90 bulbils collected from the 1999-growing season. Thirty of these bulbils were marked with fingernail polish for identification and then placed in meter squared quadrats within the Thompson Woods populations. The quadrats were examined each week to determine how many of the bulbils were still present, how many had germinated, and to measure plants growing from these bulbils. The position of each bulbil was marked with an adjacent stake-wire flag that had the measurements and number of eyes of the bulbil on it. Field survivorship of marked bulbils was analyzed using t-tests to compare means between bulbils that grew and bulbils that did not grow for each of the independent variables - bulbil length, bulbil width, and number of eyes.

The other 60 bulbils measured were planted in individual pots with Promix® (Atech Products Inc., Supply, NC) potting soil in the greenhouse on

April 28, 2000. The measurements of each bulbil were recorded on the pot in which it was planted. The pots were arranged in a 2*3 factorial randomized block design. The 2 treatments were fragmentation and fertilizer. Fertilization was chosen as a treatment because invasive plant species are often reported as opportunistic in situations of increased nutrient availability and also because *D. oppositifolia* has been used as an indicator species for soil eutrophication (Mun *et al.* 1996). The effects of fragmenting bulbils were chosen for investigation because *D. oppositifolia* was reported to occur along roadsides where the bulbils might be chopped up by a tiller and also to understand if a bulbil would be capable of germination and growth if it was partially eaten by an animal. Fragmentation was achieved by slicing the bulbils with an X-Acto® (Hunt Corporation, Boston, MA) knife. The fragmentation treatment consisted of a control group (no fragmentation), a group with 33% of the bulbil removed, and a group with 66% of the bulbil removed. The fertilizer treatment consisted of a control group that received no fertilizer and a fertilized group that received 1ml of Schultz® (Schultz Company, Bridgeton, MO) 10:15:10 liquid plant food per liter of water every seven days. There were 10 bulbils planted in each treatment combination. The plants that grew from the bulbils were measured 16 times (14, 17, 20, 26, 29, 32, 35, 39, 42, 46, 49, 53, 56, 63, 77, and 140 days after planting). The number of leaves and the stem length from the soil surface to the end of the longest stem were measured for each plant on these 16 occasions. The number of bulbils produced per plant was counted upon harvesting of the greenhouse plants. The plants were harvested on August 9, 2000 then cleaned and dried at 80° C for

48 hours. The plants were separated into roots, shoots, tubers, and bulbils and weighed.

Performance of plants grown from bulbils in the greenhouse was analyzed using two-way ANCOVA for the dependent variables of number of bulbils, leaves and stems produced, and dry weight of the bulbils, roots, shoots (leaves and stems), and tubers as well as the total dry weight. Initial size of the bulbils planted (bulbil volume) was included in the analysis as a covariate following the method of Cody and Smith (1997). Since RGR (measured by stem length) was calculated on 16 occasions, repeated measures analysis was used for RGR as described earlier. A Dunn–Sidak adjustment made the critical alpha level 0.01 but this had no effect on the outcome of ANOVAs.

A study of the effects of herbicide treatment on the success of bulbils was conducted by applying 10 % Rodeo® glyphosate (a nonselective, systemic herbicide) to bulbils in the field in July, 2000. The treated bulbils were then collected along with untreated bulbils from the same site and 20 of each were planted in individual pots with Promix® (Atech Products Inc., Supply, NC) potting soil in the greenhouse on October 25, 2000. The pots were arranged systematically in a split plot design. Plants were monitored weekly for germination and growth (measured as stem length and number of leaves produced) until June 17, 2001.

Chi-square analysis was used to examine the differences in the number of treated and untreated bulbils that germinated in the herbicide study. A t-test was performed on the heights of plants grown from treated vs. untreated bulbils.

Dispersal of the bulbils was examined by placing 0.1 m^2 quadrats at 2 m intervals along transects of the Douglas Dr. population and the Landreth I population in January and March 2001. The number of bulbils in each quadrat was counted then multiplied by 10 to get an estimate of the number of bulbils m^{2-1} at each distance from the center of the parent population. Placement of the traps covered a radius of 30 m from the centers of the parent populations. The number of bulbils found in the traps at each distance was counted.

A preliminary investigation of herbivory on *Dioscorea oppositifolia* was made in using the 57 plants that were tagged in the field. The leaves of each plant (if the plant had more than 20 leaves, then 20 leaves were randomly selected from that plant) were examined at the time of harvest (August, 2000) for evidence of herbivory. The proportion of these leaves that showed damage from herbivores of any kind was calculated and the mean damage to each leaf was visually estimated following the method used by Brown *et al.* (1987) where leaf damage is ranked on a scale from zero to six (Table 4). The mean leaf damage score was multiplied by the proportion of leaves damaged then divided by six to find the mean damage to each plant (Gange *et al.* 1989).

One-way ANOVA was used to compare differences in the amount of herbivore damage to leaves of *D. oppositifolia* among the six subpopulations. The means for all analyses are reported as means ± standard error (SE).

Table 4. Rating system for estimating the amount of leaf damage from herbivory (Brown *et al.* 1987).

Damage Rating	Estimated leaf area removed (%)
0	<1
1	1-5
2	6-25
3	26-50
4	51-75
5	76-99
6	100 (only petiole remaining)

RESULTS

Habitat Characteristics

Associated Species Cover

Axes 1 and 2 (eigenvalues of 0.86 and 0.76, respectively) of the Detrended Correspondence Analysis (DCA) were retained for interpretation. There was no clear separation of plots based on presence or absence of *D. oppositifolia* except at the DD site where there was no overlap at all between plots with and without *D. oppositifolia* (Fig. 2 and 3). The separation of sites appeared to follow a light gradient along axis one going from the closed canopy forest of the TW site to the more open canopy YL and LRI sites that are along roadsides on forest edges (Fig. 2). The TW plots, both with and without *D. oppositifolia*, had low axis one scores and overlapped little with plots from other sites (Fig. 3). The plots from the other sites had a great deal of overlap and did not show a clear separation (Fig. 3). This is most likely attributed to the fact that all the sites except for the TW site are along streams or roadsides where there is a gap in the tree canopy. Further separations of light intensity may be due to the aspect of the sites. For example, the LRI site had higher scores on axis 1 than LRII even though they are both roadside sites. This is probably because LRI has a south facing aspect while LRII has an east facing aspect.

Similar associate species were found at all eight sites that were surveyed. Figure 4 shows the DCA ordination of associate species and their separation along axis one and axis two. The most common associate plant species found in the *D.*

oppositifolia subpopulations are listed in Table 5. A complete flora of each site is given in the appendices.

Table 5. Most commonly occurring associate plant species in populations of *Dioscorea oppositifolia*. These are species that occurred in at least 40% of 96 experimental plots or occurred in at least 20% of the experimental plots and were found at 50% or more of the 49 sites surveyed by Basinger (2001).

Species Name	Percent of Plots Occurred In
Natives	
Toxicodendron radicans	68.7
Eupatorium rugosum	62.5
Parthenocissus quinquefolia	60.4
Fraxinus americana	37.5
Geum canadensis	33.3
Rubus pensilvanicus	29.2
Acer saccharum	27.1
Vitis spp.	26.0
Ulmus rubra	21.1
Acer negundo	20.8
Exotics	
Lonicera japonica	76.5
Rosa multiflora	41.7

Habitat Variables

Canopy cover averaged 68%, light intensity averaged 8% of full light, and soil moisture averaged 52% within the seven subpopulations in which these variables were measured (Table 6). The percent slope was low (under 10°) and aspect was variable with a northern aspect being the most frequently occurring among the seven subpopulations analyzed (Table 6).

Table 6. Habitat characteristics for seven subpopulations of *D. oppositifolia.*

	TWI	TWII	LRI	LRII	DDI	DDII	YLI	Average
Slope	6°	5°	9°	7°	2°	2°	3°	5°
Aspect	313°	315°	141°	87°	3°	3°	2°	0°
% Cover	85	84	39	54	56	69	43	61
Light Intensity (%)	1.1	2.9	41	12.3	5.3	3.1	-	11
Moisture (%)	61	44	42	62	48	39	-	49

The soil analyses of nine subpopulations of *D. oppositifolia* indicate soils that are low in potassium, high in phosphorus and calcium and very high in magnesium for all 9 subpopulations studied (Table 7). The soil pH ranged from 5.7 (moderately acid) to 7.6 (mildly alkaline) and the mean pH was 6.2 (Table 7). The mean cation exchange capacity, which determines a soil's ability to hold positively charged ions such as NH_4^+, was 11.2 ± SE 1.01 (Table 7) which is in the medium range according to McCarthy (1995). The soil texture classification for all nine of the subpopulations chosen for soil analysis was silty loam (Table 8). Loam is a soil composed of clay, sand, and some organic matter. Silty loam contains 50-80 % silt, which is sediment carried by moving water and accumulating along the banks of rivers, streams, lakes etc. (Armson 1977, Neufeldt and Guralnik 1988). The ratio of sand:silt:clay was very similar for all nine sites (Table 8). Soil samples were not taken from the Lusk Creek site but the

Soil Survey of Pope County, Illinois (Parks 1975) indicates a silty loam soil for this site as well.

Table 7. Results of soil analyses for nine subpopulations of *D. oppositifolia* in southern Illinois. Cation exchange capacity is in cmol kg^{-1}, other measurements are in mg kg^{-1}.

Site	pH	Buffer pH	P	K	Ca	Mg	Organic Matter (%)	Cation Exchange Capacity	Total N
DDI	6.1	6.74	22	102	1967	270	1.2	11.7	1401
DDII	5.9	6.73	13	89	1783	240	1.2	11.5	1115
TWI	5.8	6.7	67	127	1335	88	1.5	7.7	1565
TWII	6.9	-	68	132	1867	114	1.4	8.7	1284
LRI	6.5	-	18	77	1707	265	0.8	9.7	908
LRII	7.6	-	25	62	2741	132	0.9	12.0	1054
YLI	7.4	-	5	60	3313	211	0.8	14.8	940
YLII	5.7	6.7	15	159	1229	154	1.2	8.1	1223
Lamb	7.6	-	11	91	3909	128	1.7	16.6	1670
Mean	6.2	-	27	99.9	2205	178	1.2	11.2	1240
SE	0.3	-	8	11.2	306	23	.10	1.01	89

Table 8. Results of soil texture analysis for nine subpopulations of *D. oppositifolia* in southern Illinois.

Site	% Sand	% Silt	% Clay	Textural Classification
DDI	18	64	18	Silty Loam
DDII	22	64	14	Silty Loam
TWI	25	61	14	Silty Loam
TWII	24	64	12	Silty Loam
LRI	15	69	16	Silty Loam
LRII	21	66	13	Silty Loam
YLI	14	64	22	Silty Loam
YLII	18	62	20	Silty Loam
Lamb	20	67	13	Silty Loam

Species Richness and Abundance

Overall Species Richness

Paired sample t-tests with plots from all sites averaged together showed a significant difference (t = -5.07, DF = 76.8, P = .0001) in overall species richness between plots with *D. oppositifolia* and those without. Because the samples had unequal variances, the degrees of freedom were adjusted according to the Welch's approximate *t* procedure (Welch 1938) which gives a non-integer value. The mean number of species was 4.6 ± SE 0.16 in plots with *D. oppositifolia* and 6.9 ± SE 0.28 in plots without *D. oppositifolia.*

Richness and Abundance of Native Species

The paired t-test analyses showed that the mean number of native species was significantly higher in plots without *D. oppositifolia* at all seven sites except for the Thompson Woods site (Table 9). Percent cover of native species was significantly higher in plots without *D. oppositifolia* than in plots with *D. oppositifolia* at all sites (Table 10). The native species that were consistently found in plots with *D. oppositifolia* were *Parthenocissus quinquefolia, Toxicodendron radicans, Rubus pensilvanicus, Eupatorium rugosum,* and *Fraxinus americana.*

Table 9. Paired t-test results for mean number of native species compared between plots with and without *D. oppositifolia* at seven sites across southern Illinois. (SD = standard deviation; α = 0.05).

Population	DF	Mean ± SE With	Mean ± SE Without	T	Prob>T
Douglas Dr.	9	2.25 ± 0.22	6.75 ± 0.65	-5.86	0.0001
TWI & II	14	3.12 ± 0.23	4.12 ± 0.36	-1.54	0.073
Landreth I	7	4.75 ± 0.53	7.25 ± 0.89	-1.91	0.049
Landreth II	7	1.5 ± 0.33	3.62 ± 0.66	-2.69	0.015
York Ln.	7	1.25 ± 0.25	3.25 ± 0.54	-3.35	0.006
Lusk Creek	7	2.25 ± 0.32	8.12 ± 0.75	-7.91	< 0.0001

Table 10. Paired t-test results for mean percent cover of native species compared between plots with and without *D. oppositifolia* at seven sites across southern Illinois. (SD = standard deviation; α = 0.05). Degrees of freedom are the same as Table 7.

Population	Mean ± SE With *D. oppositifolia*	Mean ± SE Without *D. oppositifolia*	T	Prob>T
Douglas Dr.	3.37 ± 0.45	15.75 ± 2.25	-4.82	0.0006
TWI & II	5.75 ± 0.70	10.00 ± 1.15	-2.23	0.023
Landreth I	7.62 ± 1.09	15.25 ± 1.57	-3.15	0.008
Landreth II	2.12 ± 0.67	8.00 ± 1.09	-2.23	0.002
York Ln.	2.13 ± 0.64	7.50 ± 0.93	-4.82	0.0009
Lusk Creek	3.87 ± 0.62	7.62 ± 1.10	-3.02	0.005

Life History Characteristics in the Field

Out of the 60 plants that were originally tagged in the field, 57 survived to the end of the study. Two of the plants seemed to have been killed by trampling and one was lost without evidence of what became of it. The final mean stem length of the 57 survivors was 83.23 cm ± SE 13.59 cm and their mean total dry weight was 2.92 g ± SE 0.66 g. These plants produced a mean of 12.93 ± SE 2.95 leaves per meter of stem and all plants had only one stem originating from the same bulbil or tuber. No flowers were produced on any of the 60 tagged individuals. All inflorescences collected from other plants in these and other populations across southern Illinois contained staminate flowers only. Inflorescences of approximately 50 plants from seven subpopulations were observed.

Total biomass and biomass of the individual plant parts did not vary among the sites (Tables 11 & 12). The one-way analysis of variance showed no significant difference in total ($F_{5,51} = 1.47$, $P = 0.22$), root ($F_{5,51} = 1.22$,$P = 0.31$), or bulbil dry weight ($F_{5,10} = 1.29$, $P = 0.34$) of the tagged individuals among the six sites. The non-parametric one-way analysis of variance on ranks likewise found no significant difference in tuber ($F_{5,51} = 2.15$, $P = 0.074$) or shoot dry weight ($F_{5,51} = 0.98$, $P = 0.44$) among the six sites.

Table 11. Mean tuber and root dry weight compared among six subpopulations of *D. oppositifolia* in southern Illinois (SE = standard error).

		Tuber		Root	
Population	N	Mean	SE	Mean	SE
DD I	10	0.81	0.17	0.056	0.010
DD II	10	0.64	0.21	0.030	0.004
TWI	9	2.08	0.74	0.067	0.022
TWII	10	0.86	0.38	0.032	0.012
LR I	8	2.07	0.93	0.066	0.020
LR II	10	0.51	0.17	0.037	0.019

Table 12. Mean shoot and total biomass (g dw) compared among 6 subpopulations of *D. oppositifolia* in southern Illinois (SE = standard error).

		Shoot		Total	
Population	N	Mean	SE	Mean	SE
DD I	10	1.17	0.57	2.27	0.80
DD II	10	0.38	0.11	1.14	0.34
TWI	9	1.93	0.94	5.23	2.35
TWII	10	0.52	0.26	1.61	0.83
LR I	8	2.32	1.13	5.24	2.53
LR II	10	1.42	1.08	2.71	1.94

Comparison of tubers collected from Type I and Type II subpopulations showed that there were significant differences in tuber size (g dw) among the subpopulations ($F_{4,105} = 15.75$, $P < 0.0001$). Tukey's post hoc analysis revealed that tubers from LRIIA (Type II subpopulation) were significantly larger than tubers from all three of the Type I subpopulations but not significantly different from tubers from YLIIA (Type II subpopulation) (Table 13 and Fig. 5). Tubers from YLIIA were significantly larger than tubers from two of the Type I subpopulations (LR and DD) but not significantly different from the other Type I subpopulation (TW).

Table 13. Comparison of mean tuber biomass (g dw) of Type I and Type II subpopulations. Tubers used were from the 57 plants that were monitored throughout the 2000 growing season from 6 Type I subpopulations (DDI and II, TWI and II, and LRI and II) and from 2 Type II subpopulations (LRIIA and YLII). The tubers from the 6 Type I subpopualtions were combined in pairs according to study site to create 3 larger groups (LR, TW, and DD). Subpopulations without any letters (A,B, or C) in common were significantly different at from each other $\alpha = 0.05$.

Site	Tukey Grouping	N	DF	Mean	SE
DD	A	20	19	0.75	0.13
TW	A, B	19	18	1.44	0.42
LR	A	18	17	1.20	0.45
YLIIA	B, C	28	27	3.35	0.39
LRIIA	C	21	20	4.65	0.86

Repeated Measures

Repeated measures ANOVA revealed no significant difference in relative growth rate ($F_{5,51} = 0.92$, $P = 0.48$) or mean stem length ($F_{5,51} = 0.73$, $P = 0.60$) among the six subpopulations with the tagged individuals that were measured regularly throughout the 2000 growing season. Time had a significant effect on stem length ($F_{5,285} = 192.42$, $P<0.0001$). Overall, stem length was significantly greater in every time interval than it had been in the previous time interval (Fig.

6). There was not a significant time by site interaction for stem length ($F_{25,285}$ = 1.22, P = 0.22). Time had a significant effect on relative growth rate in the overall ANOVA ($F_{4,228}$ = 107.2, P < 0.0001). RGR_h was significantly lower in interval 2 than in interval 1 and significantly lower in interval three than in interval two (Fig. 7). RGR_h was not significantly different in interval four than it was in interval three (Fig. 7). There was an exponential decline in RGR_h through the growing season (Fig. 7). There was not a significant time by site interaction for relative growth rate ($F_{20,228}$ = 1.13, P = 0.32).

Bulbil Production

Mean biomass of the bulbils produced on the plants that were tagged and monitored throughout the 2000 growing season did not differ significantly among the six Type I subpopulations. Data for the one-way ANOVA of the bulbil biomass had to be log transformed because they were heavily skewed. Sixteen of the 57 surviving plants (28%) produced bulbils and they produced an average of 8.97 ± SE 2.38 bulbils per meter of stem. The average stem length of the 16 bulbil producing plants was 206 cm and ranged from 47 cm to 434 cm. Only four of these plants were under 100 cm long and 10 out of the 16 (63%) were over 200 cm. Overall, these 16 plants produced a mean of 19.69 ± SE 4.25 bulbils per plant and bulbil production ranged from 5.50 ± SE 2.50 bulbils per plant in the DDII subpopulation to 34.00 ± SE 12.50 bulbils per plant in the TWI subpopulation (Table 14). ANOVA on ranks revealed no significant difference in mean number of bulbils produced among the six Type I subpopulations ($F_{5,15}$ = 0.81, P = 0.57).

Bulbil bearing vines collected from Type II subpopulations had a mean of 33.42 ± SE 3.17 bulbils per meter of stem. One-way ANOVA showed that there was significant variation in the number of bulbils produced per meter of stem among five subpopulations that included two Type II and three Type I subpopualtions ($F_{4,35,} = 13.20$, $P < .0001$). Tukey's post hoc analysis determined that each of the Type II subpopulations produced significantly more bulbils per meter of stem than any of the three Type I subpopulations (Fig. 8). The three Type I subpopulations were not significantly different from each other nor were the two Type II subpopulations statistically different from each other (Fig. 8).

Table 14. Mean (± SE) number of bulbils produced per plant and number of plants (N) producing bulbils in each of six Type I subpopulations of *Dioscorea oppositifolia*. There were 10 plants tagged and monitored for bulbil production in each subpopulation.

Site	N	Mean	SE
DDI	4	18.00	5.79
DDII	2	5.50	2.50
TWI	3	34.00	12.50
TWII	1	32.00	.
LRI	3	16.33	9.06
LRII	3	16.33	14.35
Overall	16	19.69	4.25

Fruit Production

There were no fruit produced on plants observed in the field. Flower buds appeared on isolated individuals in the populations at each site but none of the plants tagged for study produced flowers. Flowering of nearby plants began around the 25th of June and continued through the first week of July.

Dispersal of Bulbils

Dispersal of bulbils was mostly limited to within 10 m of the source populations. At the Landreth Rd. site, there was an average of 152 bulbils m $^{-2}$ within 10 m of the center of the parent population (LRIIA, a Type II) but only 3 bulbils m^{-2} in the remaining 20 m (Table 15). An average of 49 bulbils m^{-2} were found within the first 10 m of the Douglas Dr. parent population (DDI, a Type I) and 0.5 bulbils m^{-2} were found in the remaining 20 m (Table 15). The majority of bulbils were found less than two meters from the center of the parent population at each of these sites (Table 15).

Table 15. Number of bulbils found in production traps set every two meters from the center of the parent population of *Dioscorea oppositifolia* for 30 m. Bulbils were collected from the traps in January and March 2001.

Distance from Center (m)	Bulbils m^{-2} Landreth Rd.	Bulbils m^{-2} Douglas Dr.
0	775	210
2	40	185
4	5	80
6	550	60
8	390	30
10	65	20
12	5	0
14	10	0
16	5	5
18	5	0
20	0	0
22	5	0
24	0	0
26	0	0
28	0	0
30	0	0

Survivorship

Of the 15 bulbils set out in TWI, nine germinated and five out of those nine survived through the end of the growing season. Evidence suggests that an unidentified small mammal may have consumed the other four bulbils. None of the ungerminated bulbils remained in the plot after August 2. There were bite marks on both the germinated and ungerminated bulbils and rodent type holes were observed adjacent to the plots.

In the TWII plot, 10 out of 15 bulbils germinated and all 10 survived through the growing season. Three of the ungerminated bulbils remained in the plot at the end of the study and the other three were missing. There was no evidence of herbivory on the bulbils in this plot.

The t-test analyses revealed no significant difference in length ($t = 0.04$, $DF = 28$, $P = 0.48$), width ($t = -0.95$, $DF = 28$, $P = 0.17$), and number of eyes ($t = -0.54$, $DF = 28$, $P = 0.30$) of bulbils that grew and bulbils that did not grow.

Herbivory

Out of the 57 plants that were examined, 55 (96%) had at least some evidence of herbivore damage to their leaves. Most of the damage observed was removed portions of the upper and lower epidermis in a manner that is characteristic of snail browsing (Matt Whiles, pers. comm.). Snails of the Endodontidae family and their feces were found on several of the leaves from the Thompson Woods and Douglas Dr. sites. There was also damage in the form of bite marks that removed entire portions of the leaves from the edges and the interior. This was most likely attributable to caterpillar browsing (Matt Whiles, pers. comm.) although no caterpillars were observed on the plants.

The mean damage rating (including all herbivore damage) (Fig. 9) and proportion of leaves damaged per plant (Fig. 10) did not vary significantly among the six subpopulations ($F_{5,51} = 2.07$, $P = 0.08$ and $F_{5,51} = 0.91$, $P = 0.48$, respectively). The difference in mean damage per plant (determined as the percent of leaf area removed times the total number leaves damaged) was marginally significant ($F_{5,51} = 2.35$, $P = 0.05$) among the six subpopulations (Fig. 11). Tukey's post hoc analysis revealed that the mean damage per plant was significantly greater in the DDII subpopulation than the LRI subpopulation but no other significant differences were found among the subpopulations. The mean damage to each leaf (damage rating) for 405 leaves sampled was 1.42 ± SE 0.11 which corresponds to between 1 and 5 % of the total leaf area removed. The mean proportion of leaves that were damaged out of a total of 405 leaves sampled was 89.6% ± SE 2.9%. The mean damage per plant was 21.8 % ± SE 2% removal of the total leaf area of the plant.

Life History Characteristics in the Greenhouse

Out of the 60 bulbils that were planted in the greenhouse, 59 of them germinated and produced plants that survived until harvested on August 9, 2000. Two-way ANCOVA showed that original bulbil volume was a significant covariate affecting shoot (leaves and stems) biomass ($F_{1,59} = 4.13$, $P = 0.047$) but did not significantly influence number of leaves, bulbils, or stems produced nor total, tuber, bulbil, or root, biomass.

Fertilization had a significant effect on the mean number of leaves produced per plant ($F_{1,58} = 13.64$, $P = 0.0005$) with the fertilized plants producing more leaves than the unfertilized plants (Fig. 12). The mean number of leaves produced in the fertilized and unfertilized treatment groups was 60.5 ± SE 7.2 and 27.2 ± SE 5.1, respectively (Fig. 12). Fragmentation did not affect leaf production significantly ($F_{2,58} = 0.57$, $P = 0.57$). The mean number of leaves produced in each fragmentation group was 47.4 ± SE 7.9 for unfragmented, 42.1 ± SE 9.3 for 33 % removed, and 42.0 ± SE 8.4 for 66% removed. There was not a significant interaction effect between fertilization and fragmentation ($F_{2,58} = 0.45$, $P = 0.63$). Plants grown with fertilizer produced more leaves than unfertilized plants at all levels of fragmentation (Fig. 13). Overall, the mean number of leaves per plant was 43.85 ± SE 4.88.

Neither the main effects nor the interaction effect were significant for the number of stems that were produced per bulbil ($F_{6,59} = 0.95$, $P = 0.47$). The overall mean number of stems produced per bulbil was 2.0 ± SE 0.1.

Tuber biomass (g dw) was significantly influenced by both fertilization ($F_{1,57} = 17.42$, $P = 0.0001$) and fragmentation ($F_{2,57} = 5.30$, $P = 0.008$). Fertilized plants produced tubers with greater mean dry weight (5.08 g ± 0.50g) than unfertilized plants (2.63 g ± 0.37 g) (Fig. 14). Tukey's post hoc analysis of tuber biomass showed that tubers grown from unfragmented bulbils were significantly larger than tubers from 66% fragmented bulbils but not significantly different from tubers grown from 33% fragmented bulbils (Fig. 15). The dry weights of tubers grown from 66% and 33% fragmented tubers were not significantly different from each other. There was not a significant interaction effect ($F_{2,57}$ = 0.75, P = 0.47) on tuber dry weight. There were 58 out of 59 greenhouse plants that produced tubers and the mean dry weight of those tubers was 3.85 g ± SE 0.35 g.

Fertilized plants had significantly greater ($F_{1,59}$ = 7.14, P = 0.01) mean root biomass (0.75 g dw ± 0.10 g dw) than unfertilized plants (0.40 g dw ± 0.07 g dw). Bulbil fragmentation was not a significant factor affecting root biomass ($F_{2,59}$ = 1.27, P = 0.29) and there was not a significant interaction between fertilization and fragmentation ($F_{2,59}$ = 1.09, P = 0.34). The mean biomass of the roots produced by the 59 greenhouse plants was 0.57 g ± 0.06 g dry weight.

Fertilization had a significant effect ($F_{1,59}$ = 10.69, P = 0.002) on shoot (leaves and stems) biomass but fragmentation did not ($F_{2,59}$ = 0.83, P = 0.44) and there was not a significant interaction between the two main effects ($F_{2,59}$ = 0.09, P = 0.92). The mean shoot dry weight of fertilized plants was greater than that of unfertilized plants over all levels of fragmentation (Fig. 16). The overall mean shoot biomass of the 59 *D. oppositifolia* plants grown in the greenhouse was 1.97 g ± 0.11 g dry weight.

Both fragmentation ($F_{2,58}$ = 3.46, P = 0.04) and fertilization ($F_{1,58}$ = 6.87, P = 0.01) were significant factors affecting total biomass of the greenhouse *D. oppositifolia* plants. Fertilized plants had significantly greater mean total biomass (10.80 g dw ± 1.23 g dw) than unfertilized plants (5.36 g dw ± 0.84 g dw) (Fig. 17). Tukey's post hoc analysis showed that mean total biomass of plants grown from unfragmented bulbils was significantly greater than that of plants grown from 66% fragmented bulbils but was not significantly different from that of plants grown from 33% fragmented bulbils (Fig. 18). The mean biomass of plants grown from 33% fragmented bulbils was not significantly different from that of plants grown from 66% fragmented bulbils (Fig. 18). There was not a significant interaction effect ($F_{2,58} = 0.32$, $P = 0.73$) on total biomass. The mean total biomass of the 59 *D. oppositifolia* plants that grew in the greenhouse was 8.08 g ± SE 0.82 g dry weight.

Repeated Measures

Repeated measure ANOVA showed that bulbil volume was a significant covariate affecting stem length (Table 16). The effect of bulbil volume on change in stem length was significant in the sixth ($F_{1,30} = 8.59$, $P = 0.0075$) and seventh ($F_{1,30} = 4.42$, $P = 0.0467$) time intervals only (between days 32 – 35 and days 35 – 39, respectively). Fragmentation also had a significant effect on stem length but the fertilization effect was not significant with bulbil volume included in the model (Table 16). There was not a significant interaction effect between fertilization and fragmentation (Table 16). Overall, fertilized plants had longer stems than unfertilized plants (Fig. 19) although this difference was not significant. Plants grown from unfragmented bulbils had longer stems than both the plants grown from 66% and 33% bulbil fragments (Fig. 20). The difference in the change in stem length among the fragmentation treatments was significant ($F_{1,30} = 7.12$, $P = 0.003$) in time interval three (days 20 - 26) but not in any other time interval.

Time had a significant effect on stem length ($F_{15,450} = 261.02$, P = <0.0001) with stems growing longer over time (Fig. 21). The changes in stem length were significant in 8 out of 15 time intervals (days14 – 17, 17 – 20, 20 – 26, 26 – 29, 29 – 32, 32 – 35, 35 – 39, and 63 – 77). There was a significant interaction between time and fertilization ($F_{15,450} = 1.85$, P = 0.028) with the difference in stem length between fertilized and unfertilized plants becoming greater over time (Fig. 19). There was not a significant interaction between time and fragmentation ($F_{30,450} = 1.34$, P = 0.11).

The main effects of fertilization and fragmentation did not significantly influence RGR_h (Table 17). Plants grew at approximately the same rate under all levels of the treatments (Fig. 22 and 23). Bulbil volume was not a significant factor influencing RGR_h (Table 17).

RGR_h varied significantly through time ($F_{14,480} = 4.54$, $P < 0.0001$) with significant differences in RGR_h occurring in 3 out of 14 contrasts (Fig. 24). Time did not have a significant interaction effect with fertilization ($F_{14,480} = 0.69$, P = 0.79) or fragmentation ($F_{28,480} = 1.10$, P = 0.33) (Fig. 18 and 19). The three-way time*fertilizer*fragmentation interaction was non-significant as well ($F_{28,480} = 0.43$, P = 0.99).

Table 16. ANOVA summary for the effects of the covariate bulbil volume along with the treatments of fertilization and fragmentation on stem length of *D. oppositifolia* plants grown from bulbils in the greenhouse. ($\alpha = 0.05$)

Source	DF	F Value	Pr > F
Bulbil Volume	1	13.48	0.0013
Fertilizer	1	3.45	0.0759
Fragmentation	2	8.77	0.0015
Fertilizer * Fragmentation	2	0.27	0.7658
Error	23		

Table 17. ANOVA summary for the effects of the covariate of bulbil volume and the treatment effects of fertilization and fragmentation on RGR_h of *D. oppositifolia* plants grown from bulbils in the greenhouse. ($\alpha = 0.05$)

Source	DF	F Value	Pr > F
Bulbil Volume	1	0.56	0.4627
Fertilizer	1	1.71	0.2040
Fragmentation	2	0.25	0.7809
Fertilizer * Fragmentation	2	0.18	0.8384
Error	23		

Bulbil Production

Fifty-five of the 59 (93 %) plants grown in the greenhouse produced bulbils and they produced an overall mean of 15.97 ± SE 2.47 bulbils per plant with a mean biomass of 0.74 ± SE 0.14 g. Fertilization had a significant effect on the mean number of bulbils produced per plant ($F_{1,55}$ = 14.46, P = 0.0004). Plants grown in the fertilized treatment produced a mean of 23.4 ± 4.2 bulbils while unfertilized plants produced a mean of only 8.5 ± 1.9 bulbils (Fig. 25). Mean biomass of the bulbils produced by the greenhouse plants was also significantly greater for fertilized plants (1.00 ± 0.24 g) than unfertilized plants (0.48 ± 0.16 g).

Fragmentation did not have a significant effect on the number of bulbils that were produced by greenhouse plants ($F_{2,55}$ = 2.63, P = 0.08) but did significantly influence the mean biomass of bulbils produced ($F_{2,55}$ = 4.83, P = 0.01). Plants grown from unfragmented bulbils tended to produce more bulbils (23.7 ± 5.6) than plants grown from 33 % or 66 % fragmented bulbils (11.6 ± 2.5 and 12.5 ± 3.7, respectively) though these differences were not significant (Fig. 26). Tukey's post hoc analysis showed that the mean biomass of bulbils produced by plants grown from unfragmented bulbils (1.25 g dw ± 0.30 g dw) was significantly greater than that of either plants grown from 33% (0.39 g dw ± 0.15 g dw) or 66 % (0.58 g dw ± 0.25 g dw) fragmented bulbils (Fig. 27).

There was not a significant interaction effect between fertilization and fragmentation ($F_{2,55}$ = 0.16, P = 0.85) on number of bulbils produced or bulbil biomass. Plants that were fertilized produced more bulbils than unfertilized plants at all levels of fragmentation (Fig. 28).

Fruit Production

Greenhouse plants did not flower and, therefore, did not produce fruit.

Herbicide Study

Chi-square analysis confirmed a significant difference in the germination frequency of glyphosphate treated vs. untreated bulbils ($\chi^2 = 21.53$, DF = 1, $P < 0.0001$). The untreated bulbils had 100% germination while the treated bulbils had only 30% germination (Fig. 29). The t-test analysis showed a significant difference in the stem lengths ($t = 3.41$, DF = 22.8, $P = 0.002$) and number of leaves ($t = 3.49$, DF = 24, $P = 0.002$) of plants grown from treated vs. untreated bulbils. There were unequal variances due to the high percentage of treated bulbils that did not germinate so the degrees of freedom for the t-tests were adjusted according to Welch's approximate *t* procedure (Welch 1938). The mean stem length was 26.95 cm ± SE 6.22 cm for plants grown from untreated bulbils and 4.37 cm ± SE 2.23 cm for plants grown from treated bulbils (Fig. 30). The mean number of leaves produced by untreated plants was 6.65 ± SE 1.38 and the mean number of leaves produced by treated plants was 1.17 ± SE 0.75 (Fig. 31).

DISCUSSION

Habitat

The environmental features and species assemblages within the subpopulations of *Dioscorea oppositifolia* analyzed in this study indicate that the most common habitat for this species is at the edges of rich, mesic forests along drainageways, and streambanks. This finding is consistent with the findings of Basinger (2001) who surveyed 54 populations in 13 southern Illinois counties. Although he observed *D. oppositifolia* growing in light levels ranging from full sunlight to full shade, the majority of the populations in southern Illinois were found at intermediate light levels along forest edges. The lack of variation in environmental features among the sites examined in this study and the high degree of overlap in the species ordination supports Hypothesis One that environmental characteristics and species associations are correlated among sites with *D. oppositifolia*.

The soil textures of the subpopulations examined are generally consistent with the soil classifications for their respective areas except for the LR subpopulations which are in an area that is predominantly silty clay loam rather than silty loam (Herman 1979). The Landreth Rd., Lusk Creek, and Lamb Rd subpopulations are also in much more gently sloping soils than is typical for their immediate area (Herman 1979, Parks 1975). The fact that all of the subpopulations were in silty soil is indicative of the species' association with streams and drainages. The soil types of these nine subpopulations are also consistent with the soils of the majority of the subpopulations examined by

Basinger (2001). These soil types differ from the predominate soil types in their respective counties, though. This suggests that *D. oppositifolia* may be specific to silty loam but more populations would have to be sampled to make such a claim with confidence. Also, soils should be compared between plots with and without *D. oppositifolia* present.

Invasive species such as *D. oppositifolia* are generally well adapted to exploitation of increased nutrient levels (Baker 1965, Grime 1977, Bazzaz 1986, Vitousek *et al.* 1996, Simberloff et. al.1997, Davis *et al.* 2000). Comparisons to the most typically reported nitrogen levels in temperate regions suggest that the *D. oppositifolia* subpopulations were growing in relatively nitrogen rich soil (Brady 1974,Young and Aldag 1982). Other studies in southern Illinois also reported lower nitrogen levels than those found in the *D. oppositifolia* subpopulations (e.g. Elsenheimer 1994, Brandon 2000). Silty loam soils tend to be relatively high in total nitrogen (Young and Aldag 1982). It is important to note that generalized standards for high and low nitrogen levels have been difficult to establish because of the volatility of the element, the high degree of variability depending on soil type and depth, and because high proportions of nitrogen are held in forms that are not available for use by plants. It is not surprising, however, that this species would be found in nitrogen rich habitats since it has been reported as an indicator species for soil eutrophication (Mun *et al.* 1996).

Disturbance is also an important element of invasion (Grime 1977, Baker 1986, Groves and Burdon 1986, Vitousek *et al.* 1996). Davis *et al.* (2000)

suggest that a community becomes invasible whenever there is an increase in the amount of resources that are not being used by the current occupants of the community. This excess in available resources can occur either through an increase in nutrient supply, such as addition of nutrient fertilizer, or by a decrease in the use of available resources such as occurs when disturbance destroys some of the resident vegetation. The subpopulations of *D. oppositifolia* in this study were all associated with some human disturbance (old homesites and roads). The benefit of disturbance to this species is probably from removal of competitors for nutrient resources rather than light resources because this species seems to require a nutrient rich environment. It does not seem to require a gap in the canopy because it grows well in closed canopy situations. Of the six Type I subpopulations that had individuals tagged and monitored throughout the growing season, the closed canopy, TWI subpopulation was the largest, had the most vigorous growth and was the closest of the six to approaching a Type II subpopulation. It also does not seem that repeated disturbance is required to maintain populations of this species since it is flourishing in pristine environments such as Big Creek Woods Memorial and Giant City Nature Preserves and Keeling Hill Natural Area (Basinger 2001). It is apparent that this species can spread from disturbed areas into surrounding areas that are not disturbed. Such is the case with populations within the Lusk Creek Natural Area and the Berryville Shale Glade Nature Preserve where *D. oppositifolia* has spread from homesites where they were planted into undisturbed natural areas (Mark Basinger, Jody Shimp pers. com.). Populations of *D. oppositifolia* were found in at least 9 state Natural Areas or Nature Preserves in a survey of the species' distribution in southern Illinois (Basinger 2001).

Species Abundance and Richness

The reduced richness and cover of associate species in the presence of *D. oppositifolia* supports the hypothesis that this species lowers species richness and abundance by eliminating native plant species and, therefore threatens the integrity of native ecosystems and could eliminate threatened and endangered plant species. Other studies have also shown reduction of native plant species in the presence of exotic species. For example, Gould and Gorchov (2000) found that the exotic shrub *Lonicera maackii* reduced survival and fecundity of three native annuals monitored. Brandon (2000) showed that the exotic perennial *Lespedeza cuneata* decreased native plant species richness in an old-field plant community. The fact that *D. oppositifolia* was associated with reduced species richness and abundance should be of great concern considering its current encroachment on many of the state's natural areas and nature preserves. It is especially alarming to note that reduced species richness and abundance was found in the presence of *D. oppositifolia* in the subpopulations examined for this study even though these were all Type I subpopulations which are much less vigorous than Type II subpopulations. A comparison of plant diversity in plots with and without *D. oppositifolia* should be made within Type II subpopulations to get a more accurate idea of how much of a threat this species really is to native ecosystems.

The probable mechanism by which *D. oppositifolia* eliminates its neighbors is competition for light. *Dioscorea oppositifolia* is capable of climbing over adjacent plants and covering them in a solid blanket of leaves in a manner similar to kudzu (*Pueraria montana* var. *lobata*). Competition for light is known to be an important factor affecting plant productivity and survival (Grime 1977, Tilman and Wedin 1982, Waller 1986, Silvertown and Lovett Doust 1993). Since vines of this species can reach an excess of four meters in length by early June, herbaceous species and tree seedlings should be especially vulnerable to shading from *D. oppositifolia.* Competition for light is asymmetric meaning that the taller plant has a disproportionate advantage over the smaller plant (Waller 1986, Sivertown and Lovett Doust 1993). This asymmetric competition is one-sided in the case of light because the shorter plant is inhibited by shading from the taller plant but the taller plant is not affected by the shorter one (Silvertown and Lovett Doust 1993). The effect of light competition could be examined in future studies by comparing the species that are present in the forest canopy with those in the understory within populations of *D. oppositifolia* where *D. oppositifolia* is clipped back in some plots and left alone in other plots.

Life History Characteristics

Stage structure refers to the relative frequency of individuals in different stages of the life cycle within a given population of plants (Silvertown and Lovett Doust 1993). Stage structure occurs where individuals of the same age, that are growing in different environmental conditions, are at completely different stages of their life cycle (Silvertown and Lovett Doust 1993). The field studies established that subpopulations of *Dioscorea oppositifolia* exhibit one of two types of stage structure and that plants of Type II subpopulations have larger tubers and produce more bulbils than plants of Type I subpopulations. It is unclear what causes this stage structure. It has been proposed that the Type II subpopulations are older and have, therefore, had more time to develop a large underground tuber that in turn produces more vigorous plants. This is reasonable because some of the Type I and Type II subpopulations are within a few meters of each other and it is easy to imagine that the Type I subpopulations are satellite colonies that have spread from the Type II subpopulation. Another factor in support of this theory is that many of the Type II subpopulations are at old homesites where the species was probably planted in the early 1900s. The problem with this theory is that plants grown from bulbils in the greenhouse were able to produce large tubers, long vines, and numerous bulbils in just one growing season. Another possibility is that the stage structure is reflective of the environmental conditions in which the subpopulation is growing. Van Groenendael and Slim (1988) found that populations of *Plantago lanceolata* exhibited stark contrasts in timing of life history stages when grown in wet vs. dry environments. *D. oppositifolia* plants grown in the greenhouse produced tubers that were larger than tubers from Type II subpopulations while unfertilized greenhouse plants produced tubers that were smaller than tubers from Type II subpoulations but larger than tubers from Type I subpopulations. This would indicate that perhaps mineral nutrients are limiting growth in some of the subpopulations but the soil analyses do not support such a claim because nutrient levels in the Type II subpopulations were not greater than those of Type I subpopulations. Still, it may be that plants growing in the Type II subpopulations are in optimal conditions for growth and reproduction while individuals in Type I subpopulations remain stunted until some crucial resource or combination of resources becomes more available in their given surroundings. It is probably a combination of the age of the subpopulations and the environmental conditions they are in that is determining their stage structure. More work needs to be done examining the differences between these two types of demographies and factors contributing to them.

In the field, plants with stems less than 1m long generally did not produce bulbils or flowers. This study supports the claim that *D. oppositifolia* does not reproduce sexually in southern Illinois and suggests the explanation is that there are no pistillate plants here.

Dioscorea oppositifolia had a high rate of survival of germinated plants both in the field and in the greenhouse. Bulbils had a high survival rate in the greenhouse but not in the field. It is well known that seeds in general have a high risk of predation, decay, and disease and, as a result, suffer a high rate of mortality especially as time since dispersal increases (Silvertown and Lovett Doust 1993, Chambers and McMahon 1994, Marone *et al.* 2000). It appears that the same may be true for bulbils of *D. oppositifolia* but, like plants producing seed, *D. oppositifolia* seems to produce more than enough bulbils to compensate for the high rate of losses.

The pattern of bulbil dispersal around the parent plants suggests that the primary dispersal agent is gravity. Bulbils were concentrated under parents and were scarce outside a 10 m radius around the parents. It is unclear how the plants are dispersed over far distances but populations were observed throughout several watersheds appearing to have dispersed by streamflow. It is unknown how isolated populations such as the ones in Thompson Woods originated but they may have started from bulbils that were carried from nearby ornamental gardens by animals. Further research on the dispersal of this species is needed to understand its pattern of spreading so as to control future invasions into new areas.

The greenhouse study revealed that this species has increased growth and reproduction with the application of fertilizer. These results are in agreement with soil analyses and observations in the field that suggest that this species performs best in high nitrogen. The greenhouse study also showed that bulbil size was relatively unimportant to the fitness of plants growing from the bulbils. Original bulbil size influenced stem growth (height) and shoot biomass but had no effect on bulbil production, tuber size or overall biomass. This means that even very small bulbils can produce plants that will grow into long vines and produce large tubers and numerous bulbils.

The greenhouse study also established that fragmented bulbils are capable of successful growth and bulbil production. Fragmentation did not affect stem growth or bulbil production and decreased tuber size only when 66% of the bulbil was removed prior to planting. This means that bulbils that are partially eaten by animals or chopped up by a tiller will still be capable of producing healthy plants that will themselves produce more bulbils.

The herbicide study gave insight into the ability to control *D. oppositifolia* with glyphosphate. Rodeo® application seemed to be very effective when applied to bulbils in the field. Only one plant that sprouted from the treated bulbils appeared to be healthy enough to eventually produce a tuber and bulbils of its own. The other two plants that sprouted from the treated bulbils had very tiny, deformed leaves and were extremely stunted. Bulbils that did not germinate completely deteriorated. It is unknown if the glyphosate treatment would effectively prevent established tubers from resprouting and since some of the bulbils in this study survived the herbicide treatment, it is likely that more than one application would be needed to eliminate a population of *D. oppositifolia.* The application of 5 % glyphosate solution to bulbils in North Carolina was less successful than the results reported here (Basinger 2001).

CONCLUSIONS

Dioscorea oppositifolia poses a serious threat to some of the most pristine habitats in southern Illinois. It can inhibit the establishment of tree seedlings and late-season perennials thereby reducing native plant diversity. This species is quickly spreading throughout southern Illinois watersheds and presents a difficult control problem on account of the large tubers and numerous bulbils it produces. Preliminary investigations using herbicides have shown some promise in controlling germination of the bulbils but it is not known if they can prevent resprouting of the underground tuber. It is likely that repeated herbicide applications would be necessary. Treating the bulbils before spring and then treating the vines (foliar application) in May, before they begin to produce bulbils, would probably be most effective. Applying herbicide to the bulbils during the dormant season would reduce risks to non-target species. This species is touted as a medicinal wonder over Internet sites that sell bulbils for propagation (personal observation). Promotion of *D. oppositifolia* for household gardens should be halted due to its invasive nature. An intensive management program should be implemented immediately to control existing populations and to prevent further spread of *D. oppositifolia*. This study finds *Dioscorea oppositifolia* to possess the characteristics of an "exotic weed" as defined by the Illinois Exotic Weed Act and recommends that the species be added to the IEWA list of "exotic weeds".

FIGURES

Figure 1. Current known U.S. distribution of *Dioscorea oppositifolia* as of 2001 (USDA National Plants Database). This species has been reported from one county in Florida.

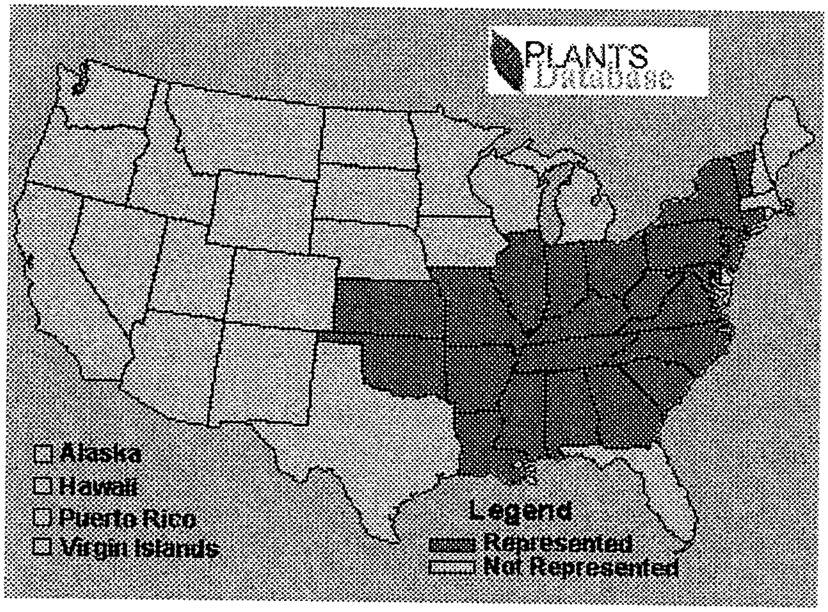


Figure 2. Detrended Correspondence Analysis. Circles = Landreth Rd. I, boxes = Landreth Rd. II, upside-down triangles = Thompson Woods, hexagons = Douglas Dr., diamonds = York Lane, triangles = Lusk Creek. Closed symbols are plots without *Dioscorea oppositifolia*, symbols with crosses are plots with *Dioscorea oppositifolia*.

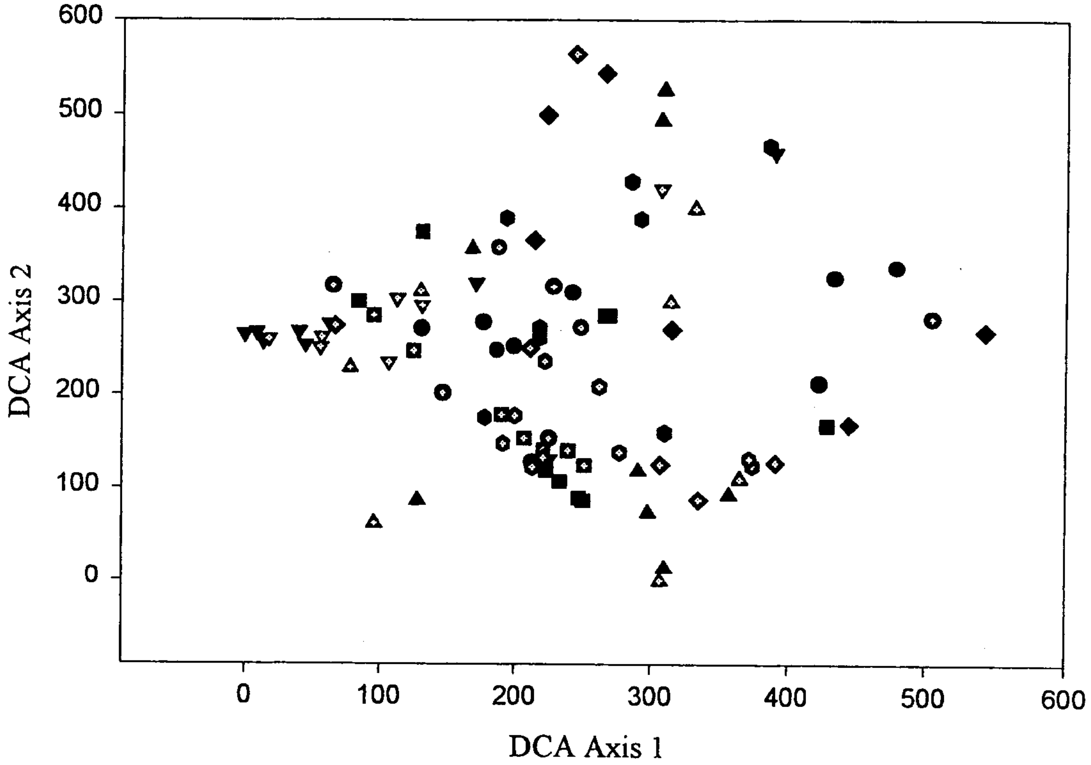


Figure 3. DCA ordination average scores (+ 95 % CI) for plots with and without *Dioscorea oppositifolia* at each of six sites across southern Illinois. A = LRI with, B = LRI without, C = LRII with, D = LRII without, E = TW with, F = TW without, G = DD with, H = DD without, I = YL with, J = YL without, K = LC with, L = LC without.

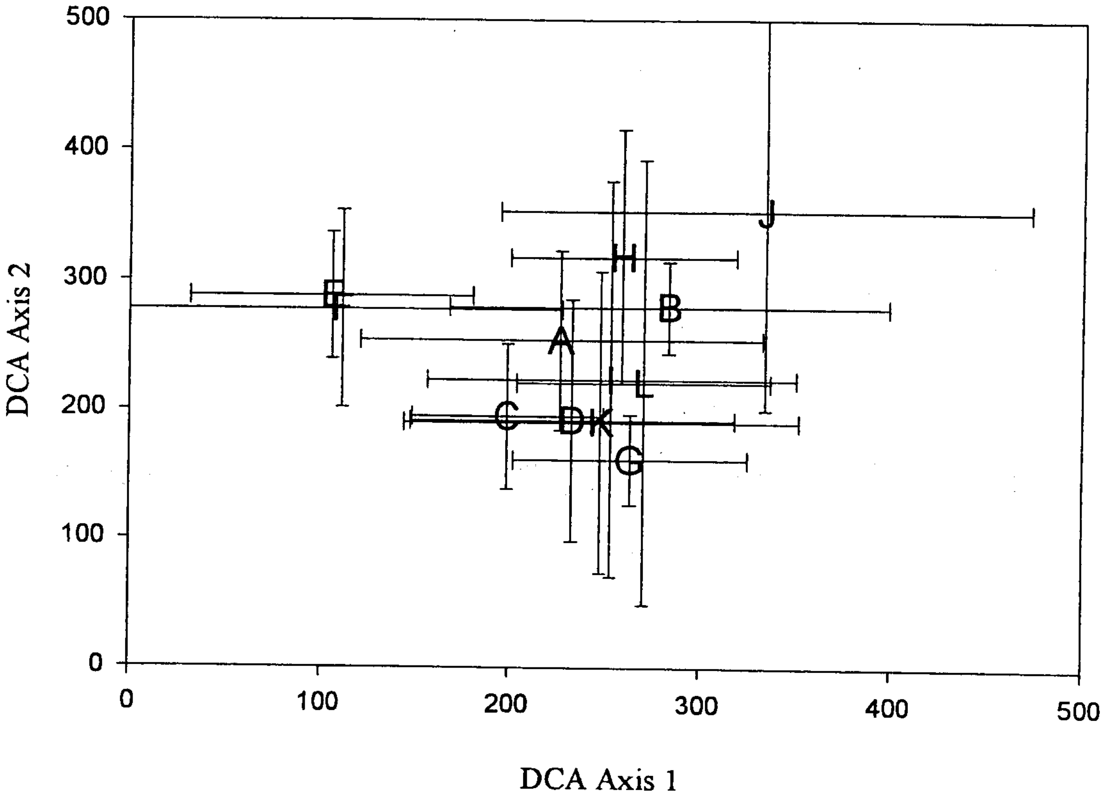


Figure 4. DCA ordination of species in plots with and without *Dioscorea oppositifolia* at six sites across southern Illinois. Scientific name for species codes are given in Appendix

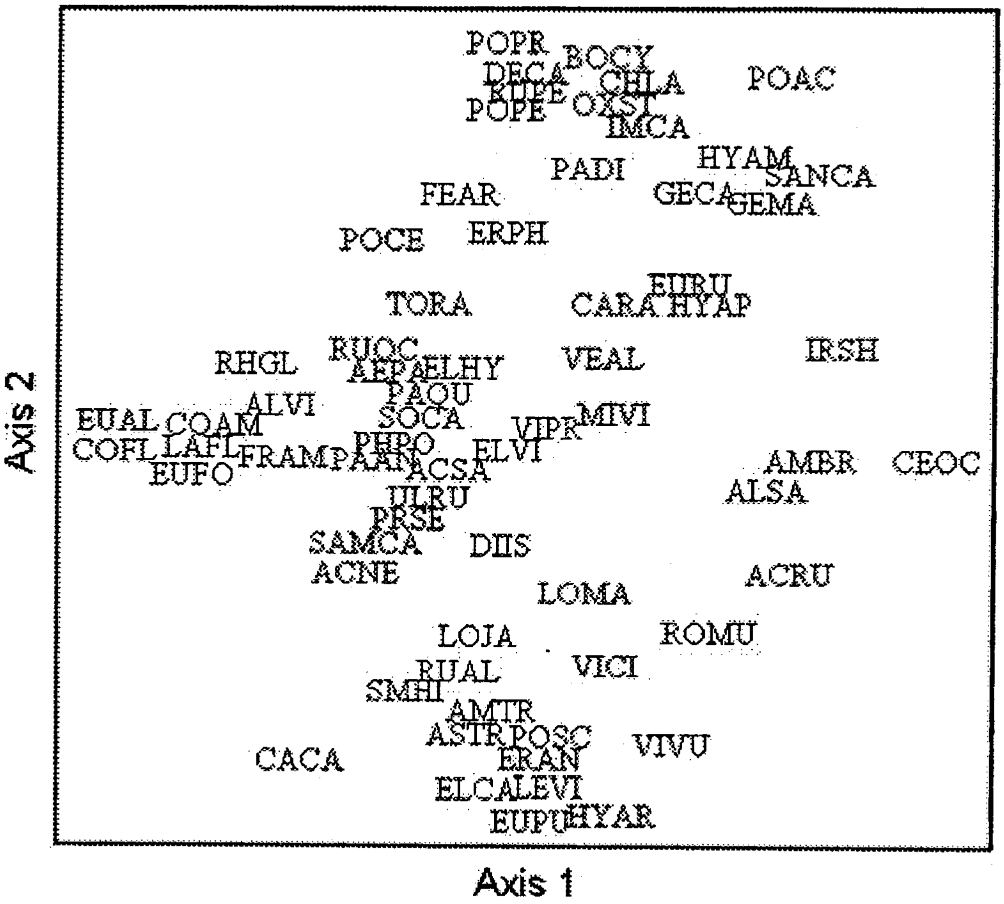


Figure 5. Comparison of mean (+ 1 SE) tuber biomass (g dw) among Type I (LR, TW, DD) and Type II (YLIIA, LRIIA) subpopualtions. Subpopulations with the same letters are not significantly different at $\alpha = 0.05$.

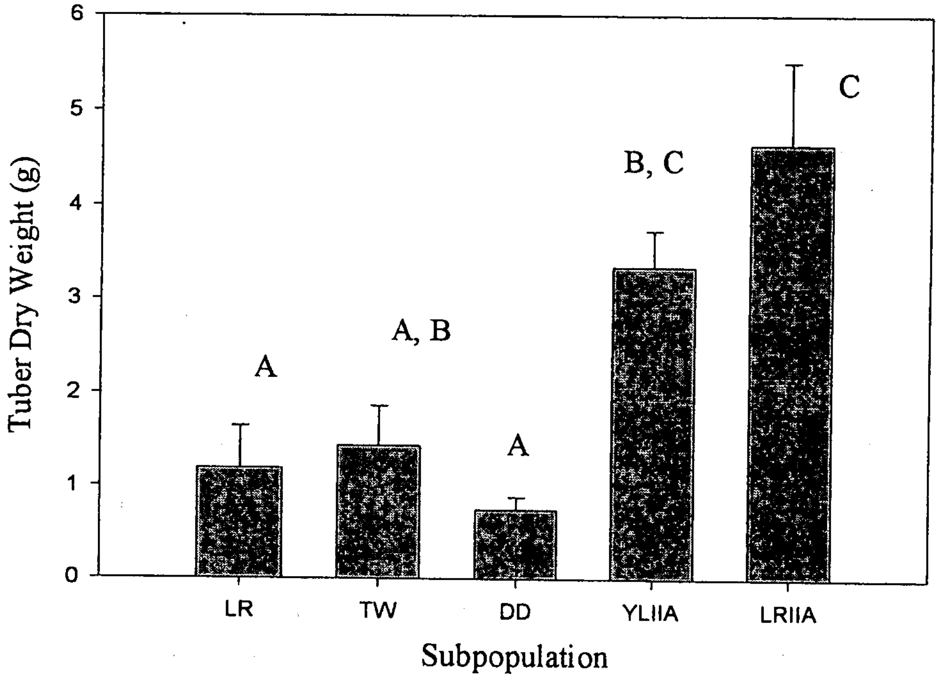


Figure 6. Mean stem length (± 1 SE) of 60 *Dioscorea oppositifolia* plants that were measured on six occasions between April 22 and August 22, 2000. There were 10 plants each measured in six subpopulations.

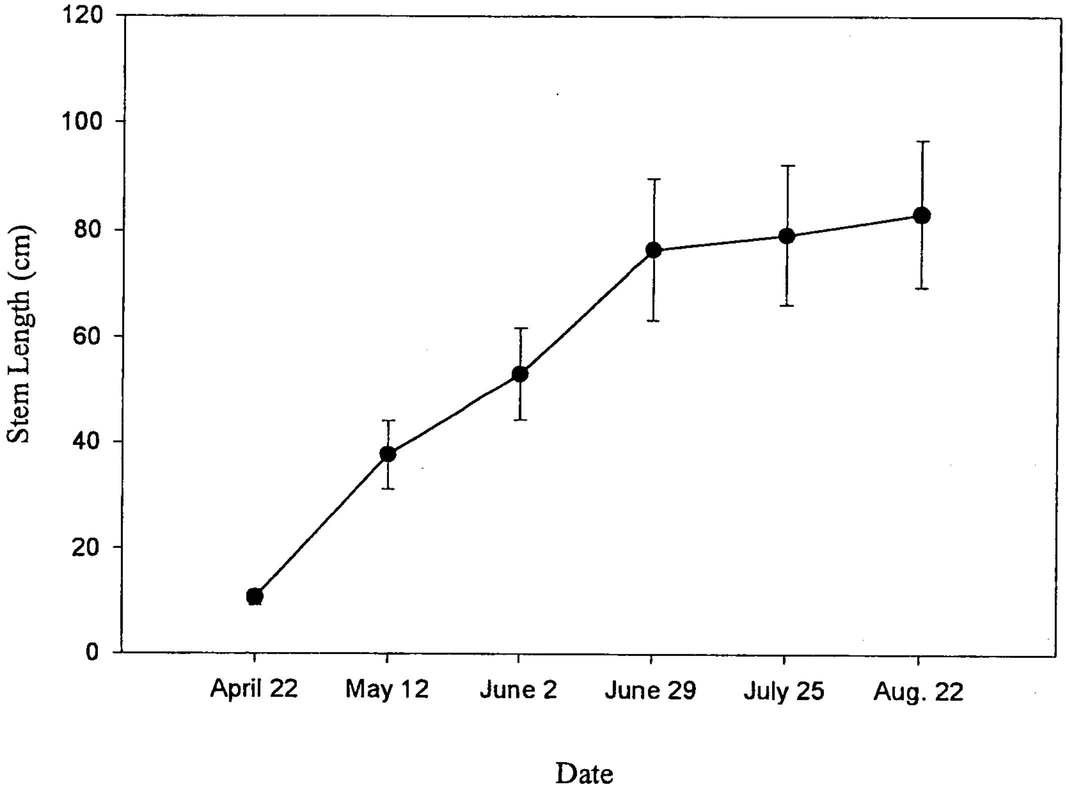


Figure 7. Mean (± 1 SE) RGR_h (calculated from stem length) of 60 *Dioscorea oppositifolia* plants in each of five time intervals. Time 1 = April 22-May 12 time 2 = May 12-June 2, time 3 = June 2-June 29, time 4 = June 29-July 25, time 5 = July 25-August 22, 2000. There were 10 plants each measured in six subpopulations.

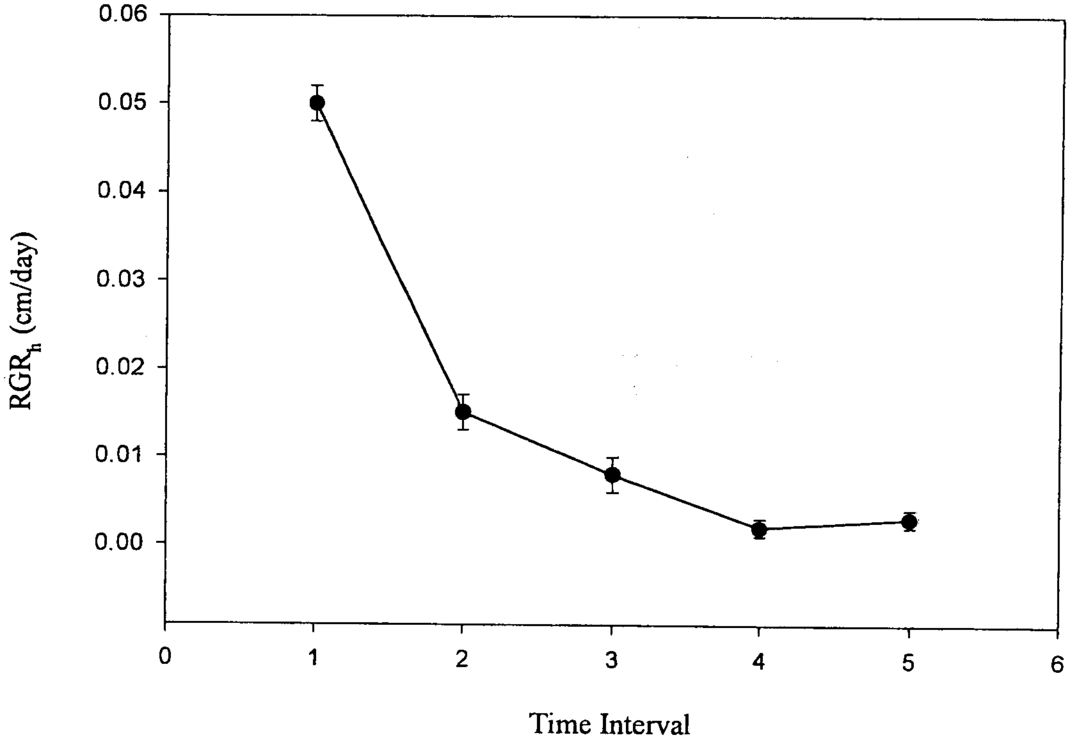


Figure 8. Mean number of bulbils per meter of stem (+ 1 SE) on *D. oppositifolia* plants in Type I (LR, TW, DD) and Type II (YLIIA, LRIIA) subpopualtions. Subpopulations with the same letters are not significantly different at $\alpha = 0.05$.

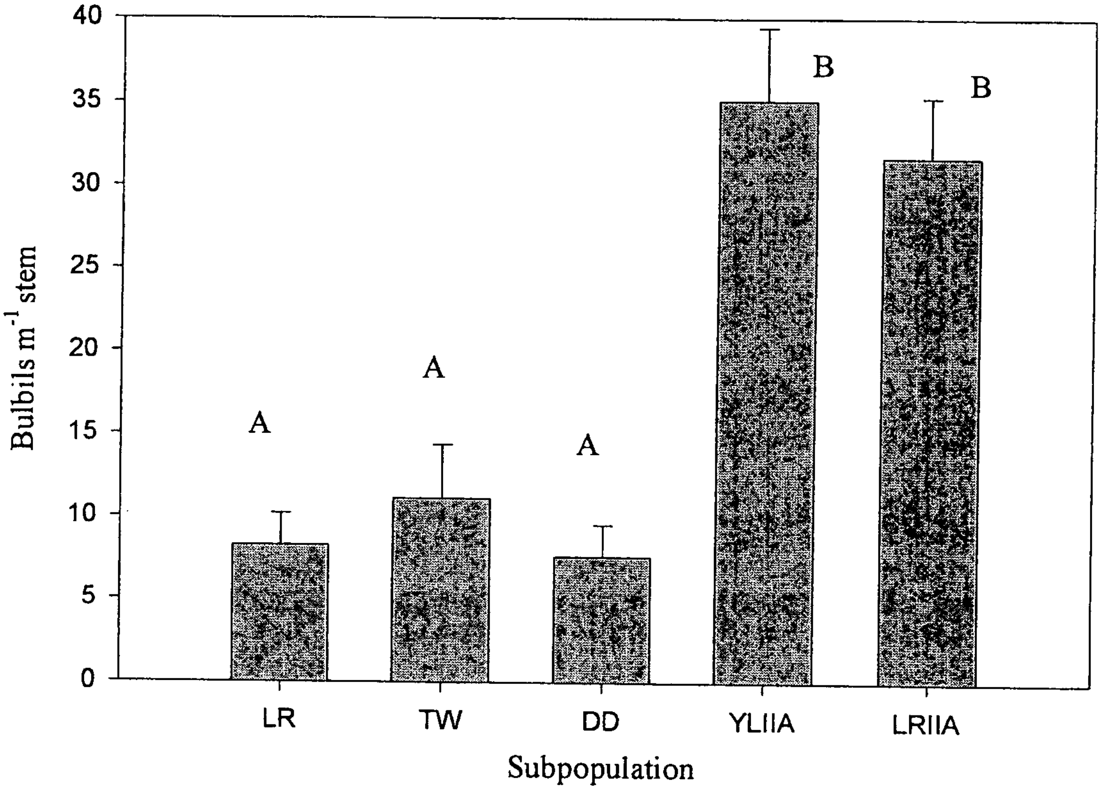


Figure 9. Mean damage rating (+ 1 SE) based on percent of leaf area removed from *Dioscorea oppositifolia* plants at each of the six Type I subpopulations in which individual plants were sampled. The damage rating is on a ranked scale from 0 - 6 where 0 < 1%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, and 6 = 100% leaf removal (Table 3).

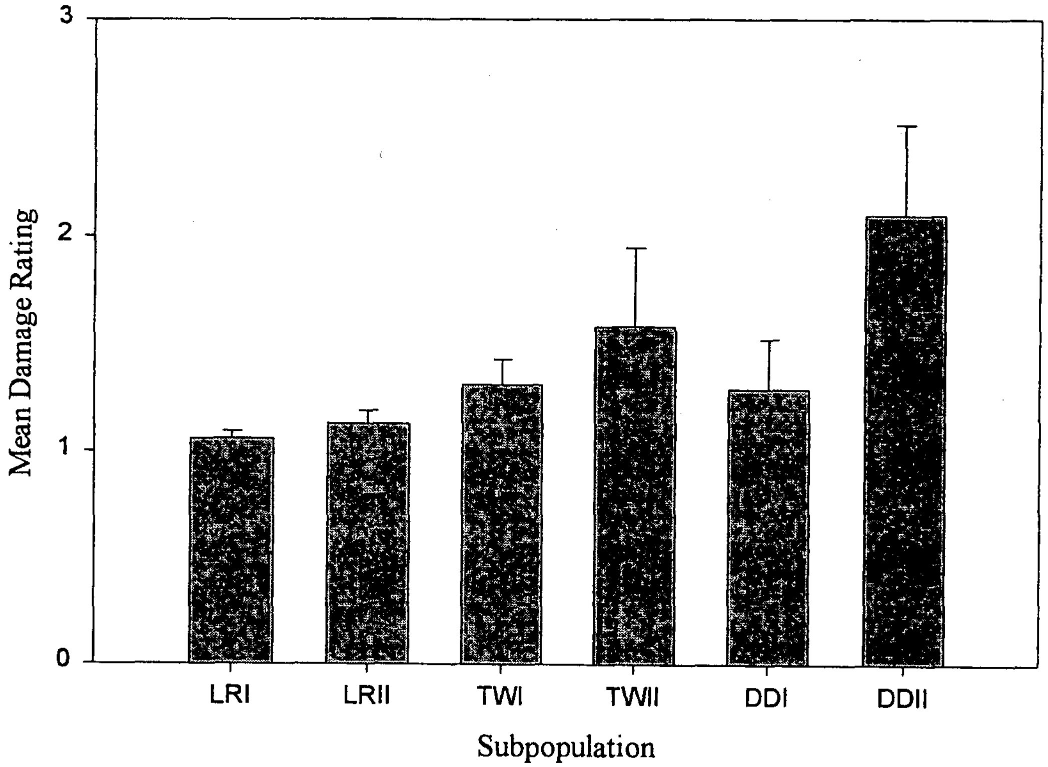


Figure 10. Mean (+ 1 SE) proportion of *Dioscorea oppositifolia* leaves damaged by herbivory at each of six Type I subpopulations. Ten plants were sampled in each subpopulation.

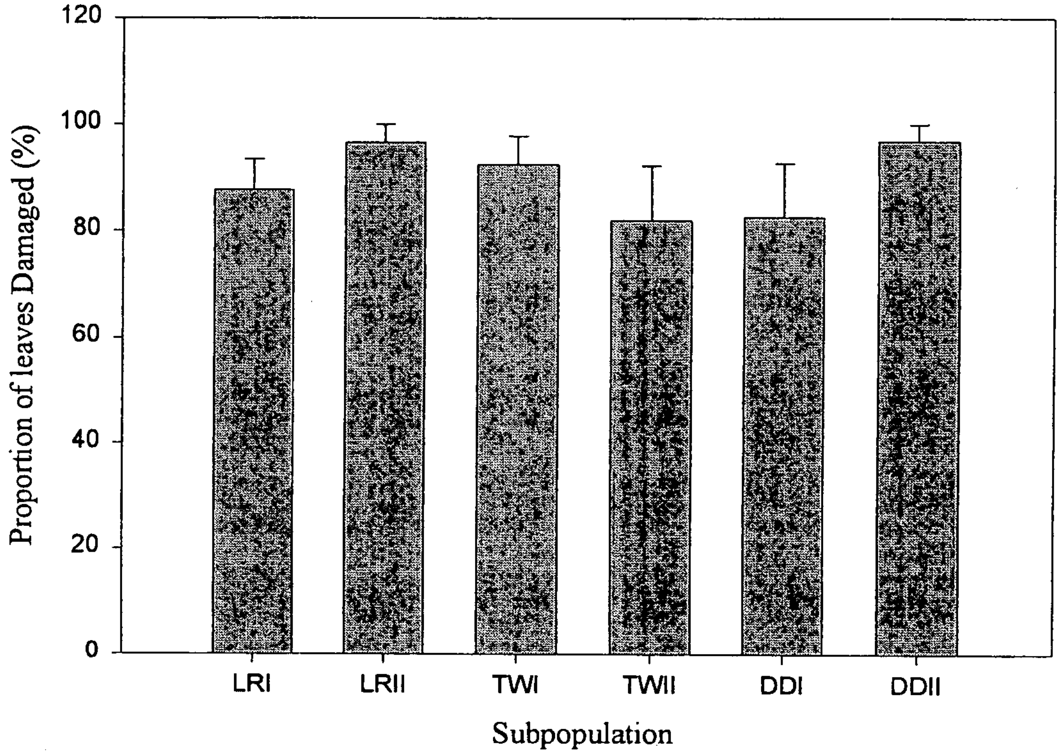


Figure 11. Mean total damage(+ 1 SE) measured as percent of leaf area removed times the total number of leaves damaged from *Dioscorea oppositifolia* plants at each of six Type I subpopulations. Damage here is any removal of leaf area that appeared to be due to herbivory. Ten plants were sampled in each subpopulation. Subpopulations with asterisks beside them are significantly different from each other at α = 0.05.

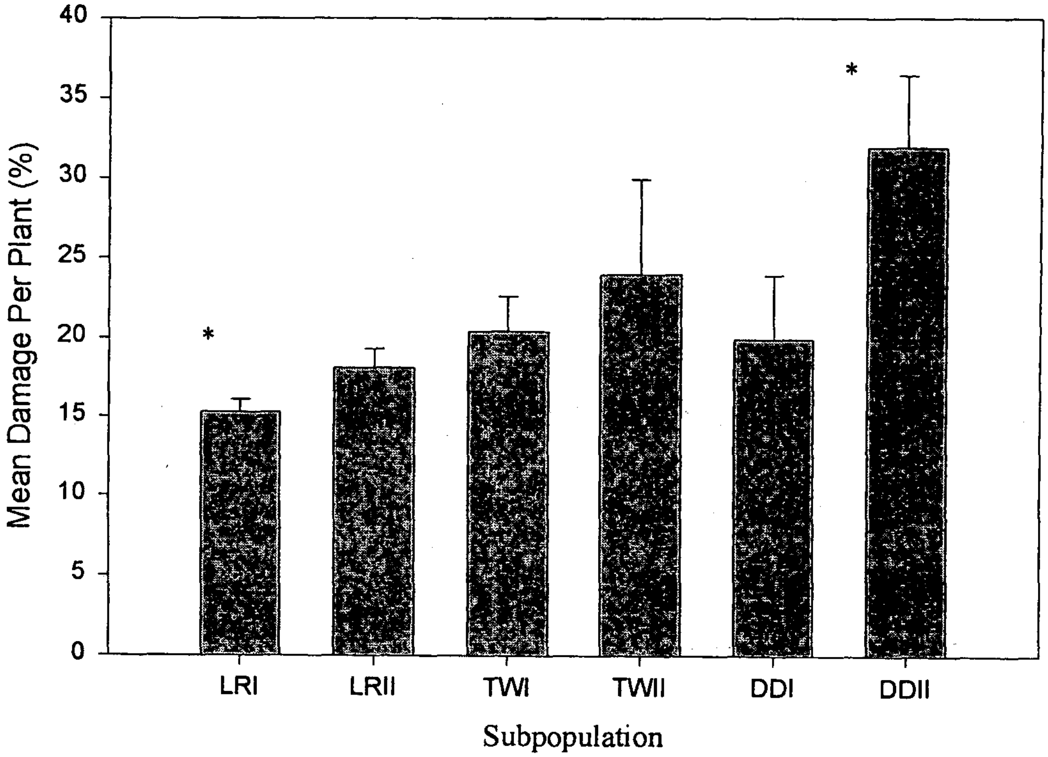


Figure 12. Mean number of leaves (+ 1 SE) produced by fertilized vs. unfertilized *D. oppositifolia* plants grown in the greenhouse.

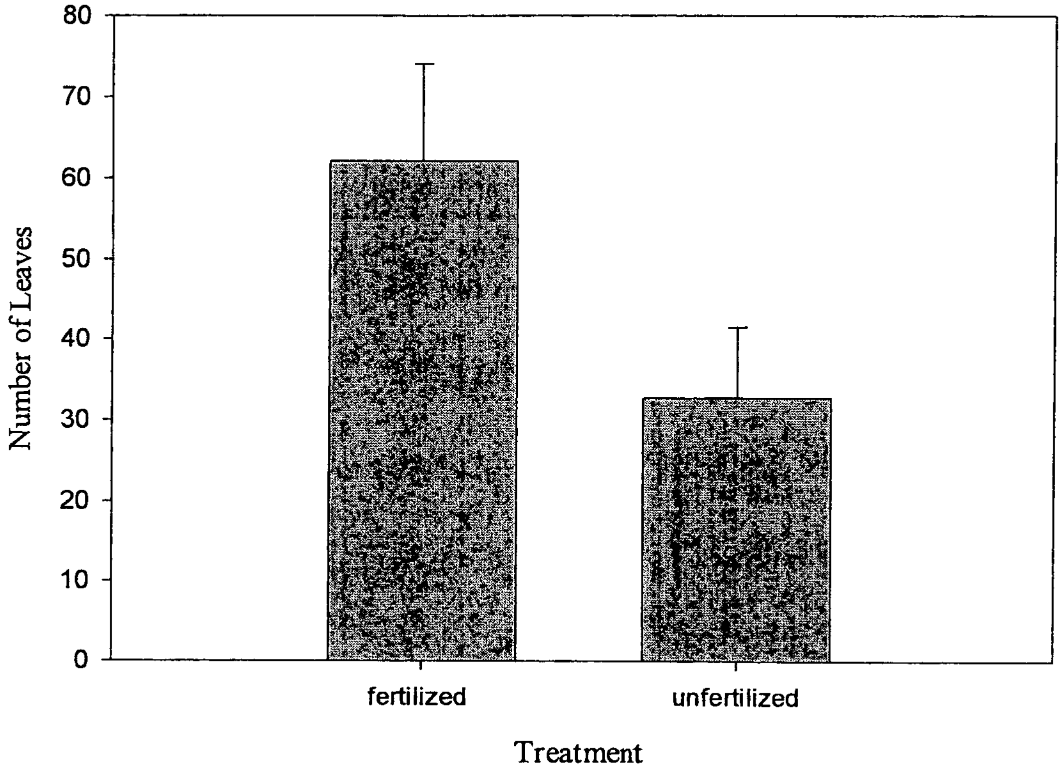


Figure 13. Number of leaves produced by fertilized and unfertilized *D. oppositifolia* plants grown in the greenhouse from bulbils with different levels of fragmentation.

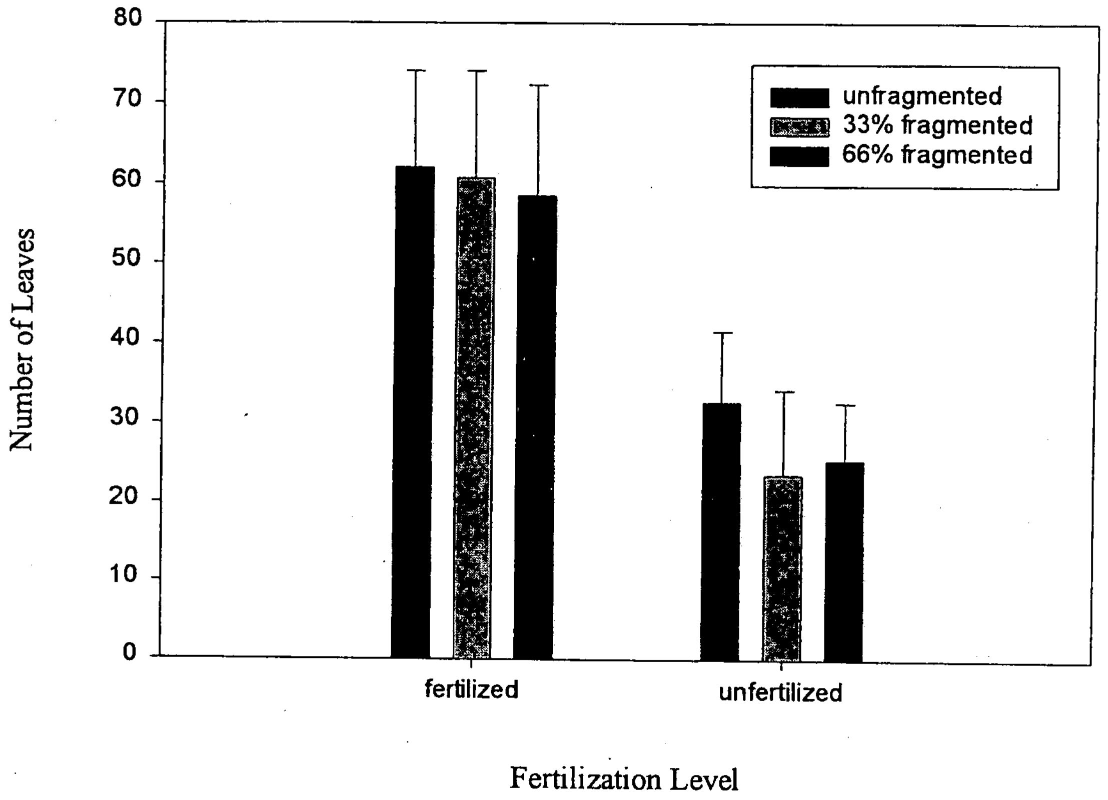


Figure 14. Mean (+ 1 SE) tuber biomass (g dw) of fertilized vs. unfertilized *D. oppositifolia* plants grown in the greenhouse .

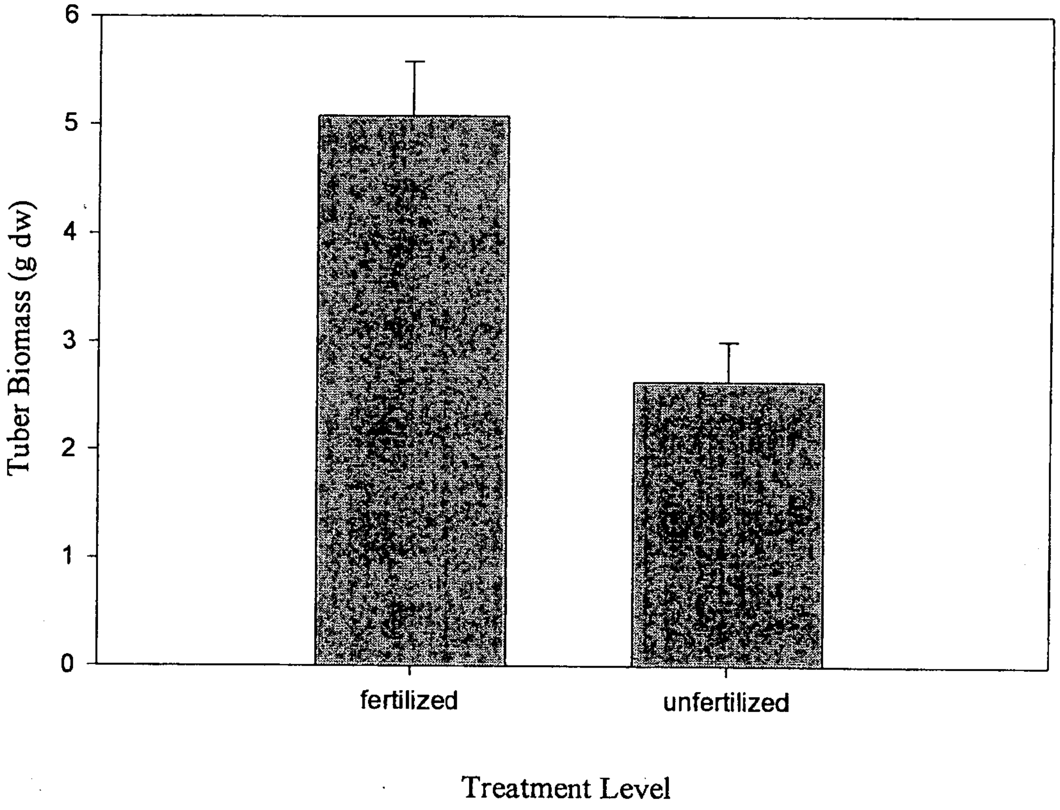


Figure 15. Mean (+ 1 SE) tuber biomass (g dw) of *D. oppositifolia* plants grown from bulbils with 3 different levels of fragmentation. Treatments with different letters are significantly different at $\alpha = 0.05$.

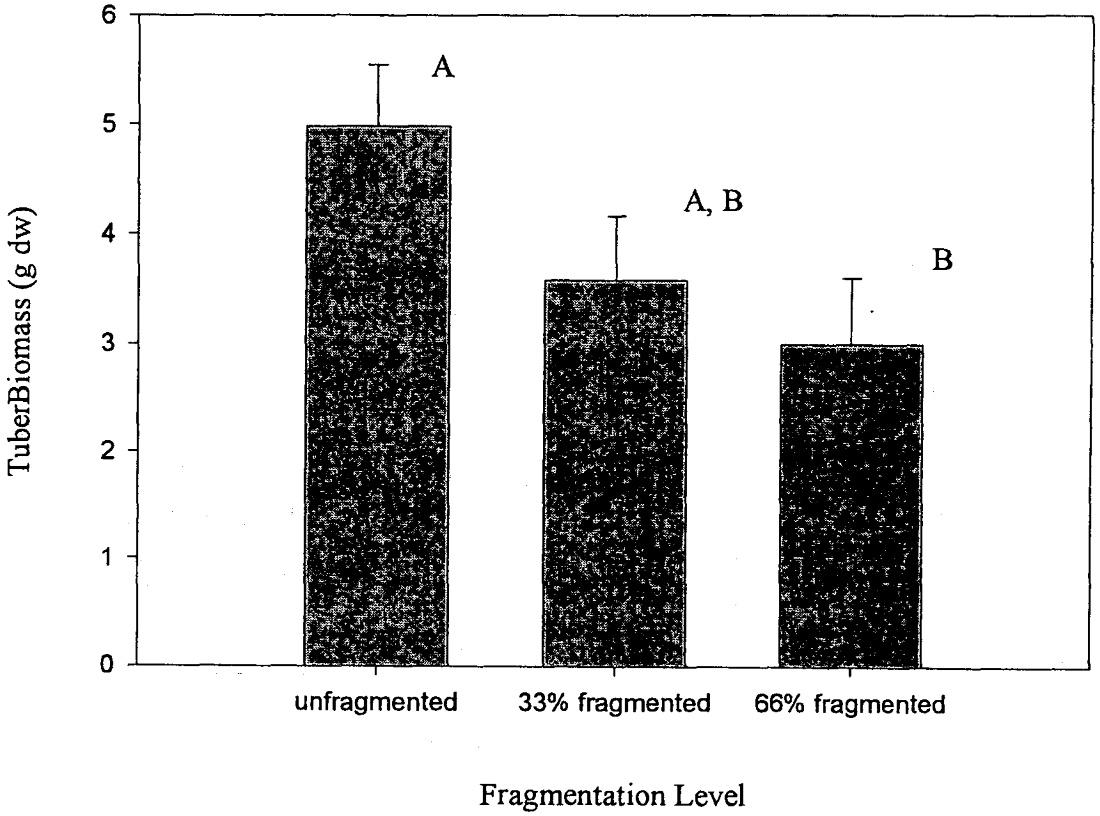


Figure 16. Mean (+ 1 SE) shoot (leaves and stems) biomass (g dw) of fertilized and unfertilized greenhouse *Dioscorea oppositifolia* plants at different levels of fragmentation.

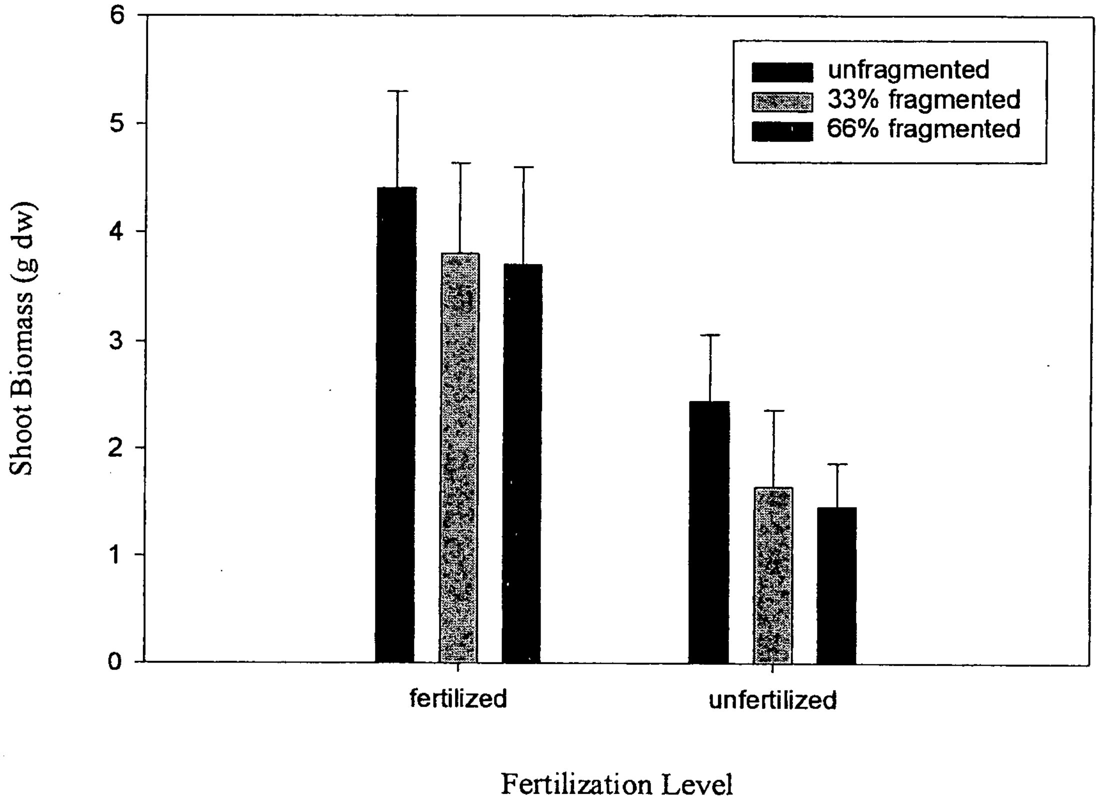


Figure 17. Mean (+ 1 SE) total biomass (g dw) of fertilized vs. unfertilized *D. oppositifolia* plants grown in the greenhouse.

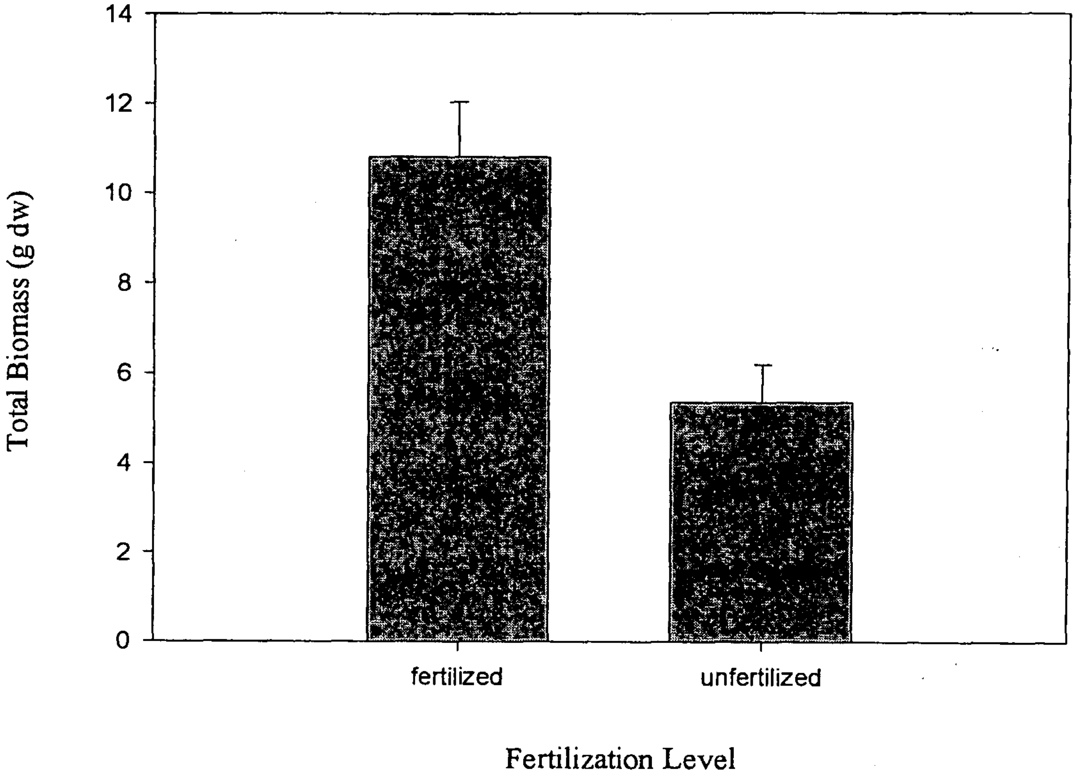


Figure 18. Mean (+ 1 SE) total biomass (g dw) of *D. oppositifolia* plants grown in the greenhouse from bulbils with different levels of fragmentation. Treatments with the same letters are not significantly different at $\alpha = 0.05$.

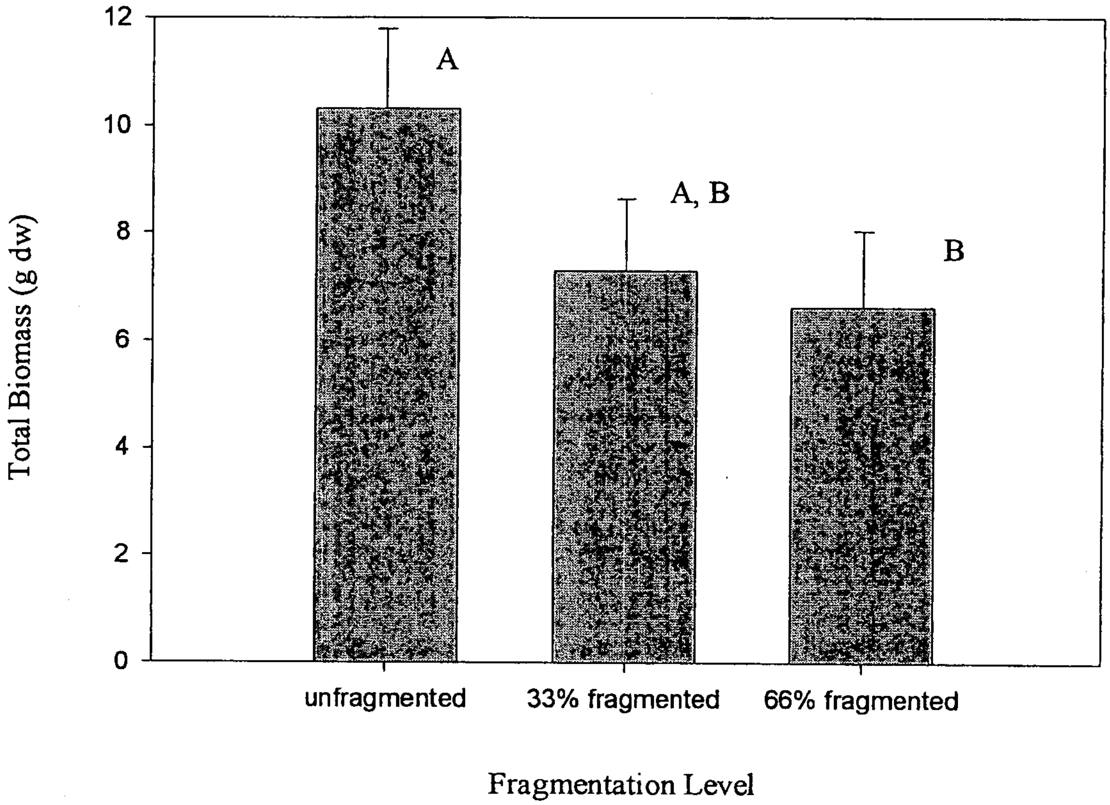


Figure 19. Mean stem length (± 1 SE) of fertilized vs. unfertilized *D. oppositifolia* plants grown in pots in the greenhouse. Time is expressed as the number of days after planting.

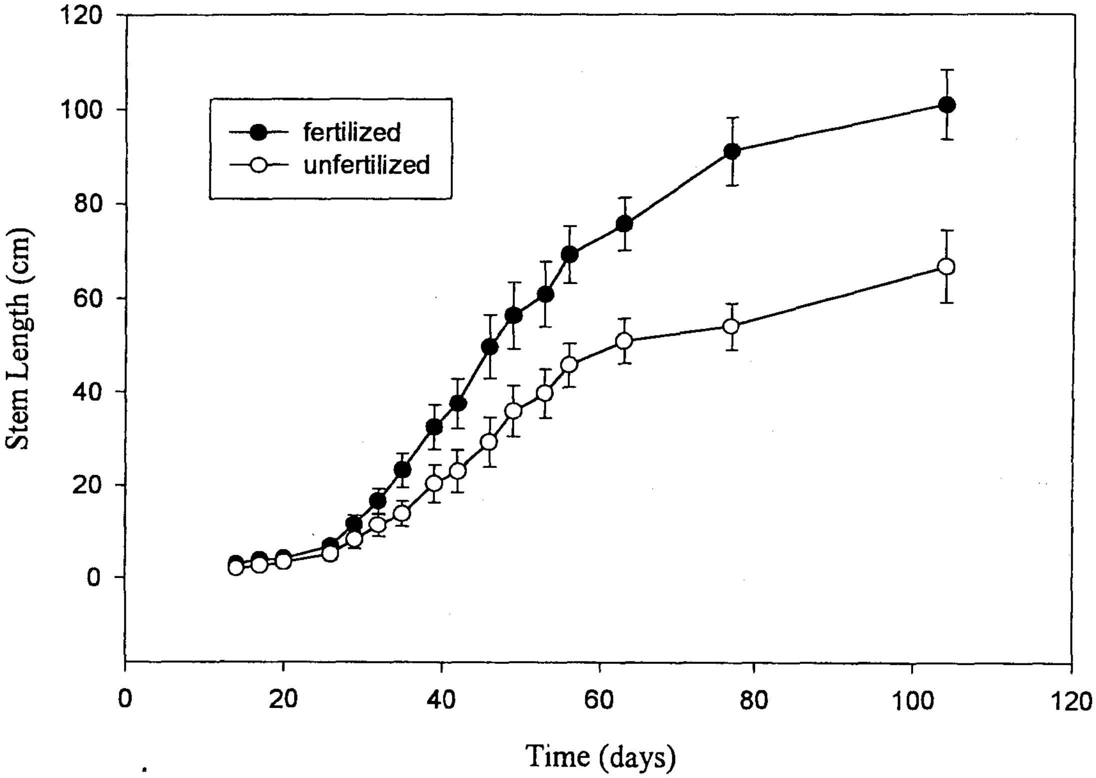


Figure 20. Mean stem length (± 1 SE) of *D. oppositifolia* plants grown in pots in the greenhouse from whole bulbils, bulbils with 33% of their mass removed, or bulbils with 66% of their mass removed. Time is expressed as the number of days after planting.

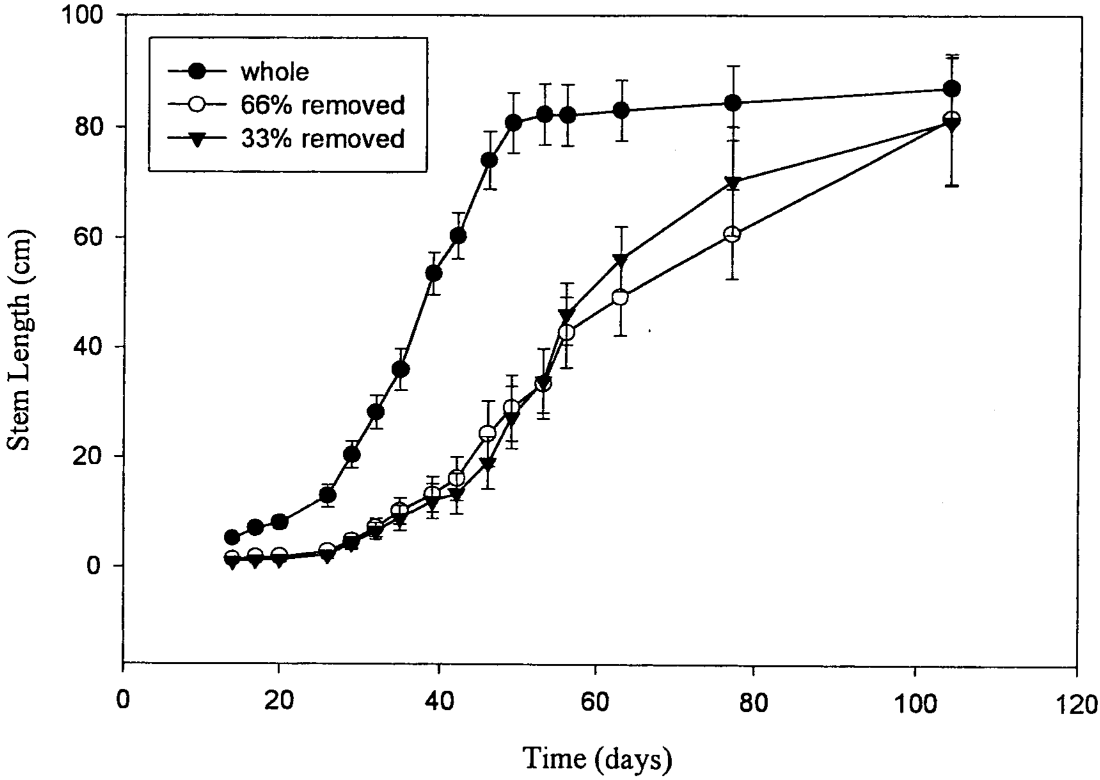


Figure 21. Overall mean stem length (± 1 SE) of *D. oppositifolia* plants grown in pots in the greenhouse. Time is in days since planting.

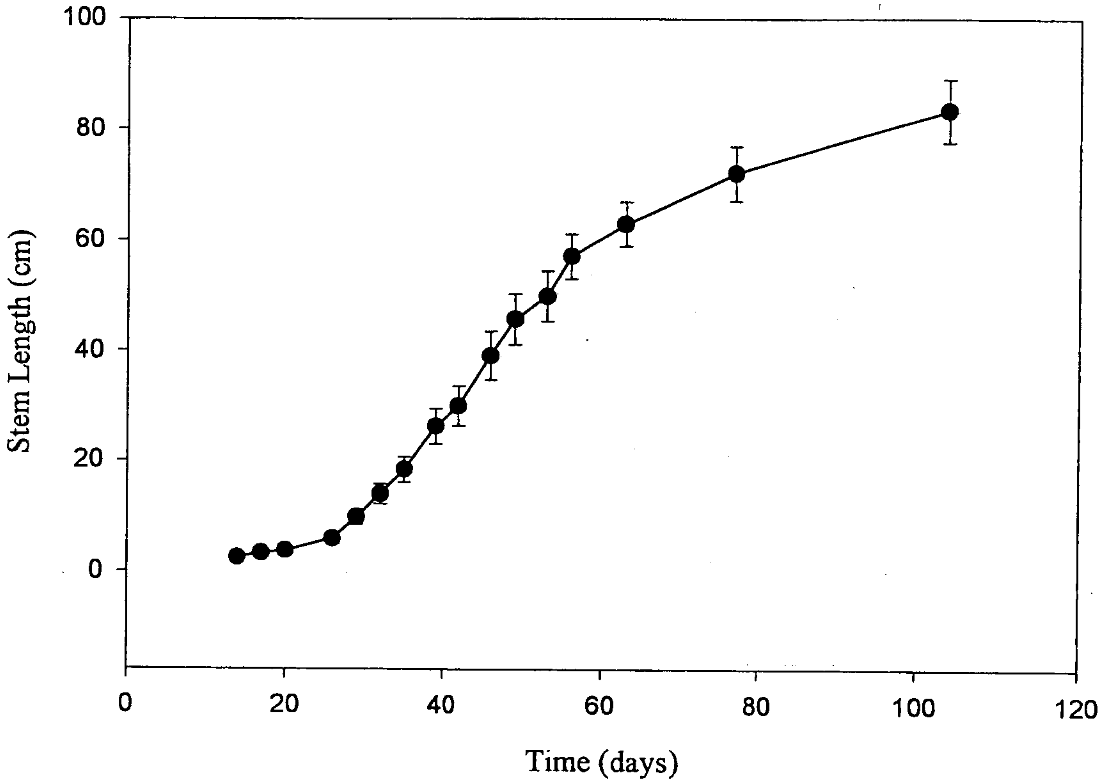


Figure 22. Mean RGR_h (± 1 SE) of fertilized vs. unfertilized *D. oppositifolia* plants grown in pots in the greenhouse. Time intervals: 1 = 14-17, 2 = 17-20, 3 = 20-26, 4 = 26-29, 5 = 29-32, 6 = 32-35, 7 = 35-39, 8 = 39-42, 9 = 42-46, 10 = 46-49, 11 = 49-53, 12 = 53-56, 13 = 56-63, 14 = 63-77, 15 = 77-104 days after planting.

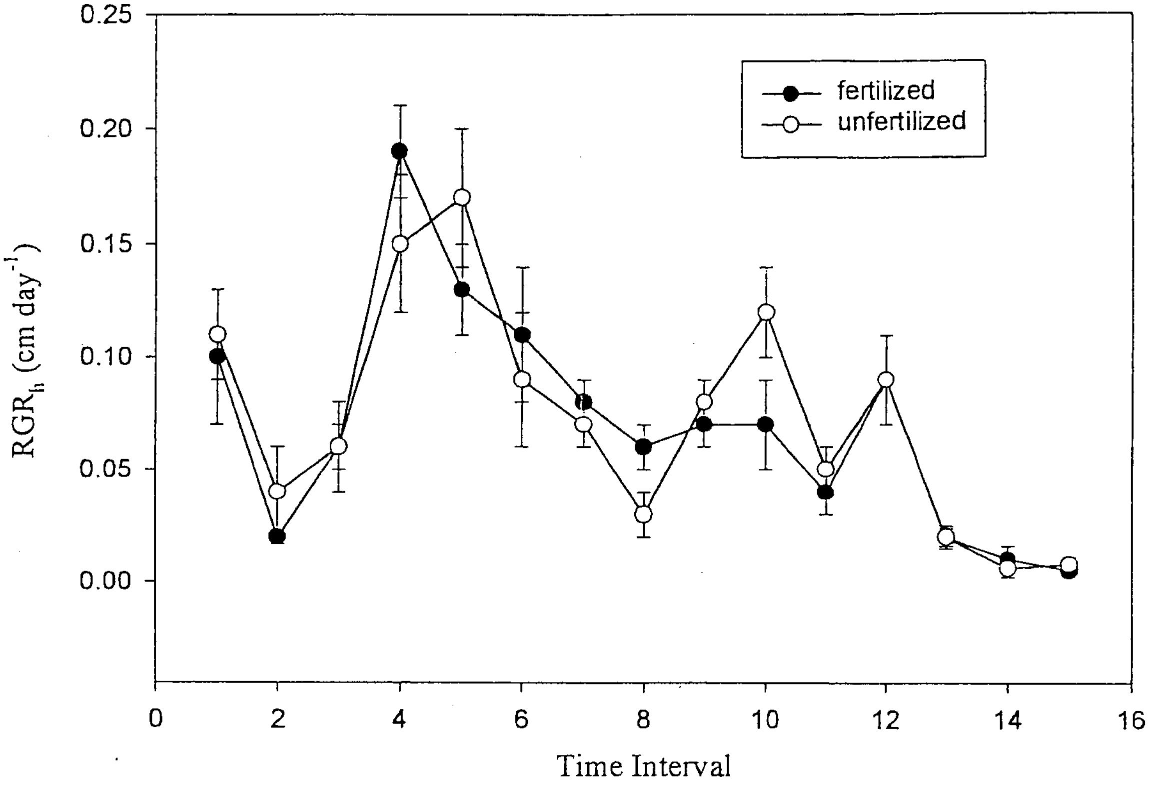


Figure 23. Mean RGR_h (± 1 SE) of *D. oppositifolia* plants grown from whole and fragmented bulbils in pots in the greenhouse. Time intervals: 1 = 14-17, 2 = 17-20, 3 = 20-26, 4 = 26-29, 5 = 29-32, 6 = 32-35, 7 = 35-39, 8 = 39-42, 9 = 42-46, 10 = 46-49, 11 = 49-53, 12 = 53-56, 13 = 56-63, 14 = 63-77, 15 = 77-104 days after planting.

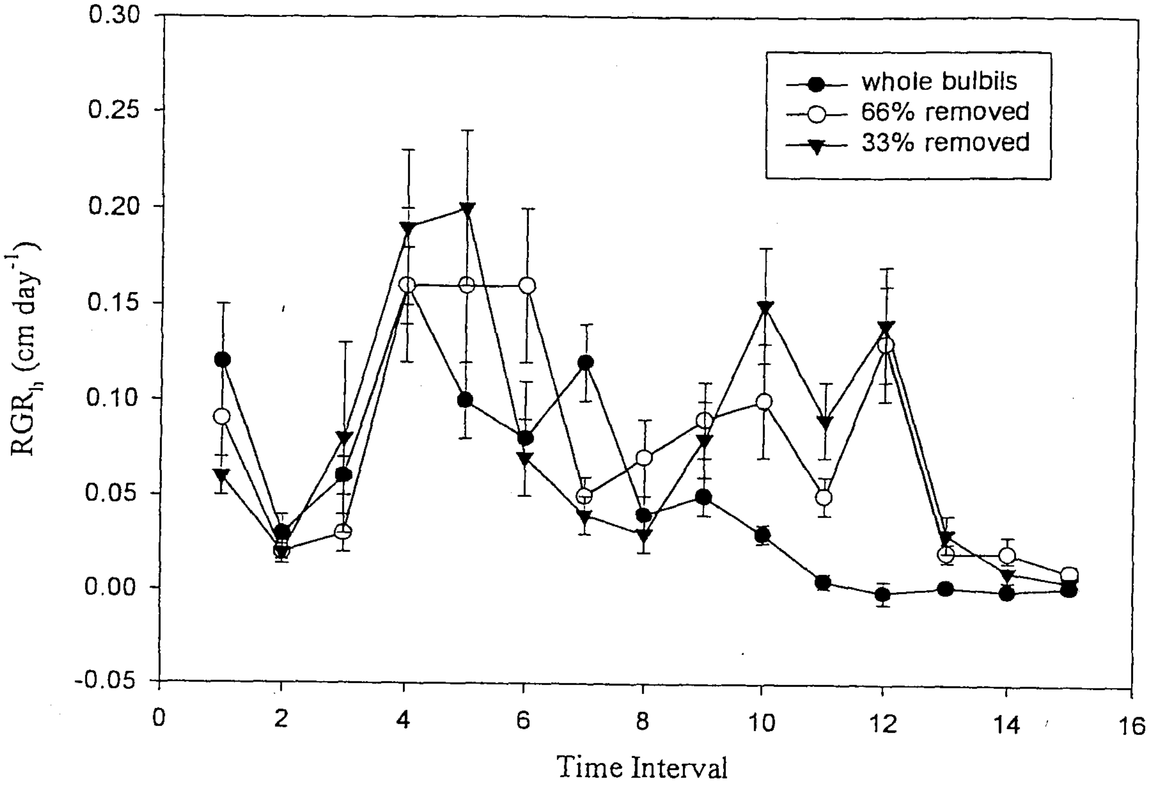


Figure 24. Overall mean RGR_h (± 1 SE) of *D. oppositifolia* plants grown in pots in the greenhouse.

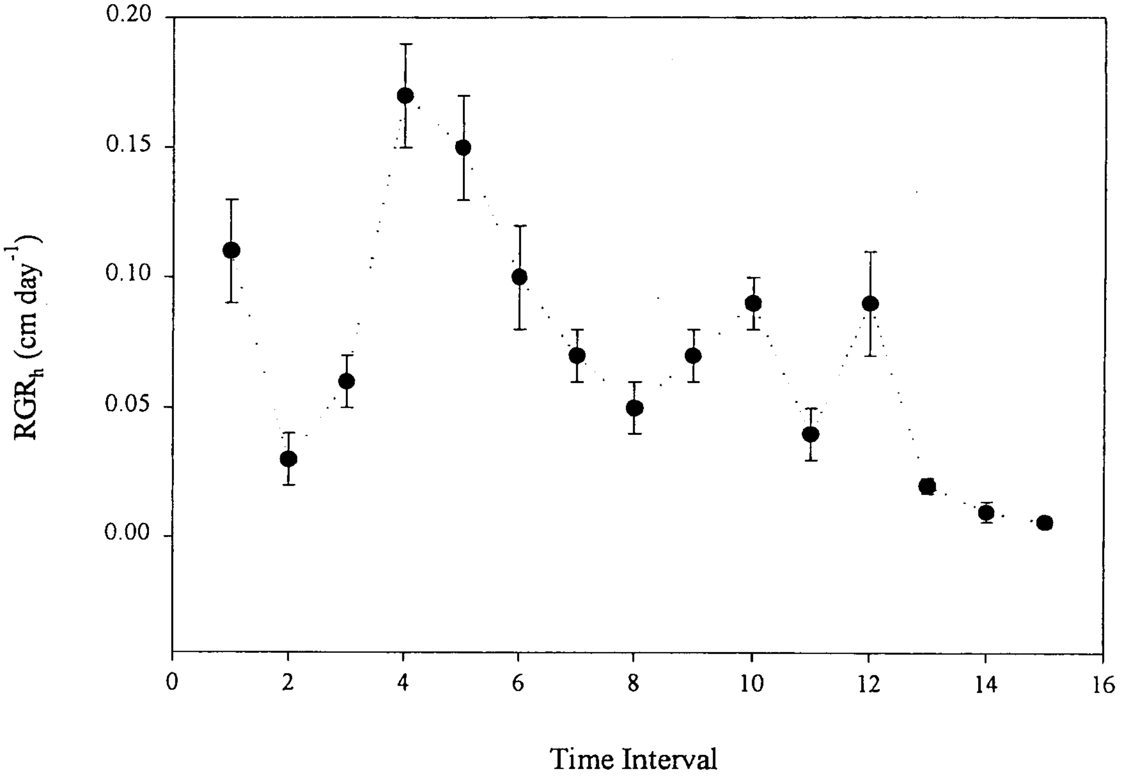


Figure 25. Mean number of bulbils produced by fertilized vs. unfertilized *D. oppositifolia* plants grown in the greenhouse.

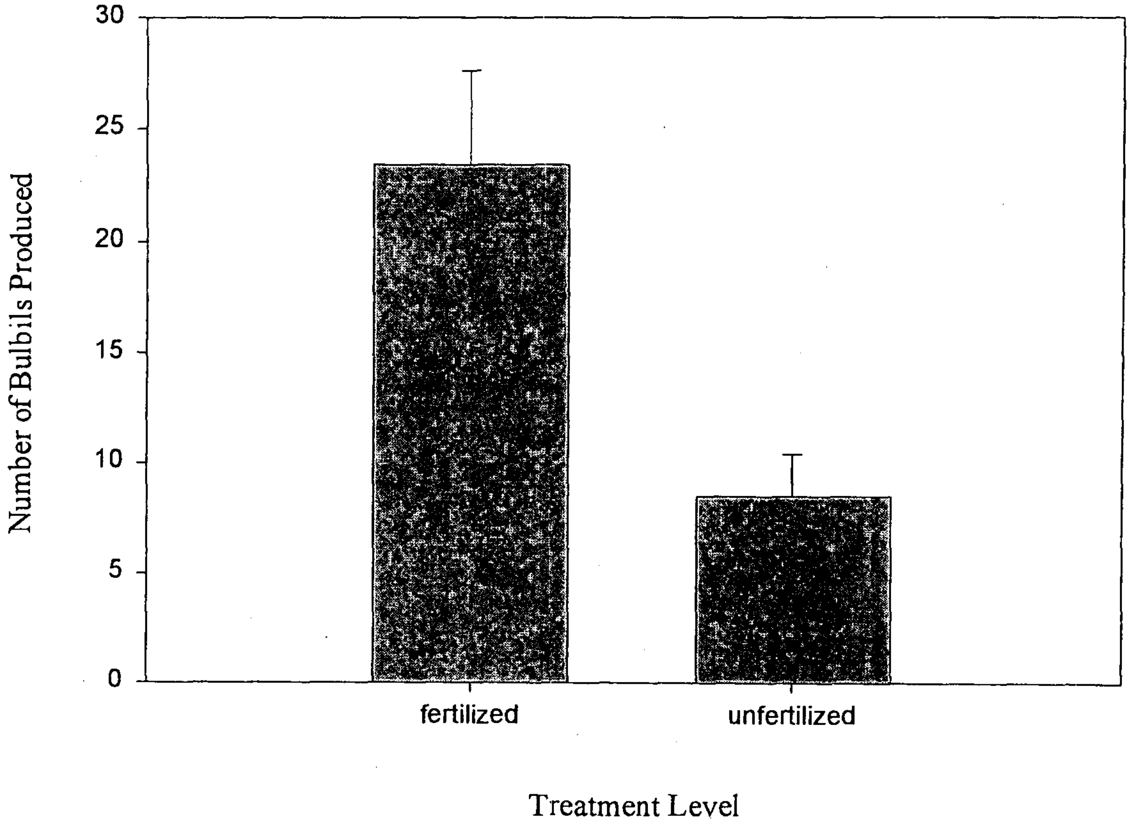


Figure 26. Mean number (+ 1 SE) of bulbils produced by *D. oppositifolia* plants grown in the greenhouse from whole bulbils, bulbils with 33% of their mass removed, or bulbils with 66% of their mass removed

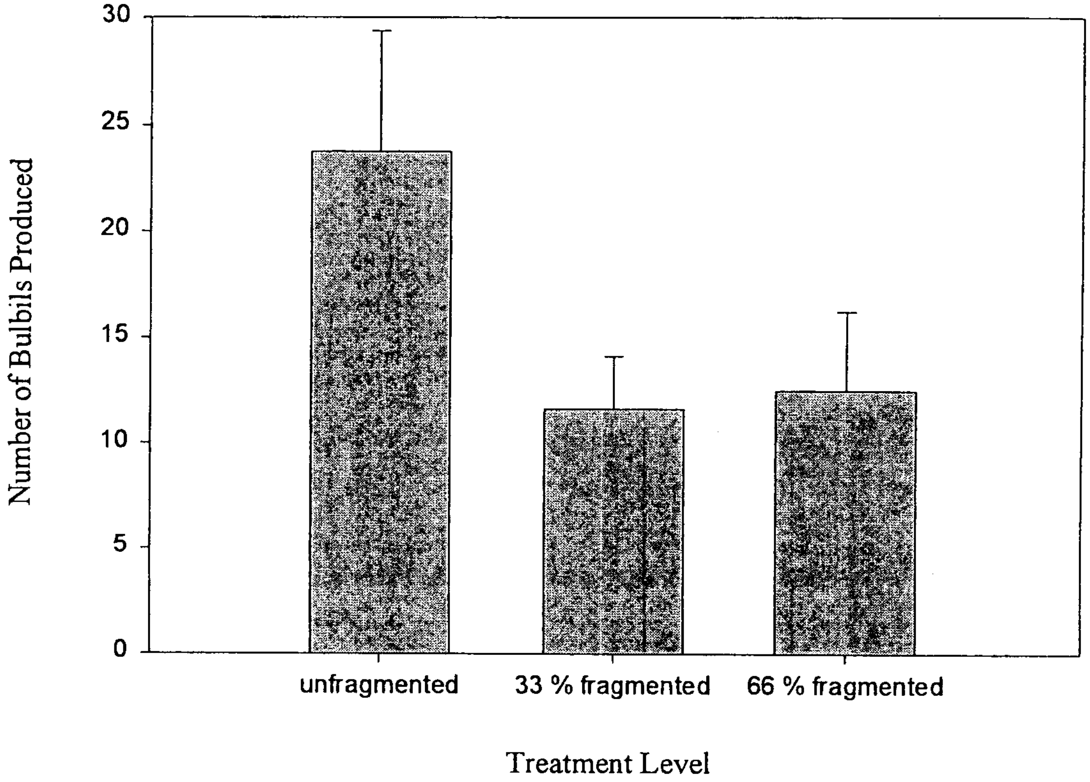


Figure 27. Mean (+ 1 SE) biomass (g dw) of bulbils produced by *D. oppositifolia* plants that were grown in the greenhouse from bulbils with different levels of fragmentation. Treatments with the same letters are not significantly different at $\alpha = 0.05$.

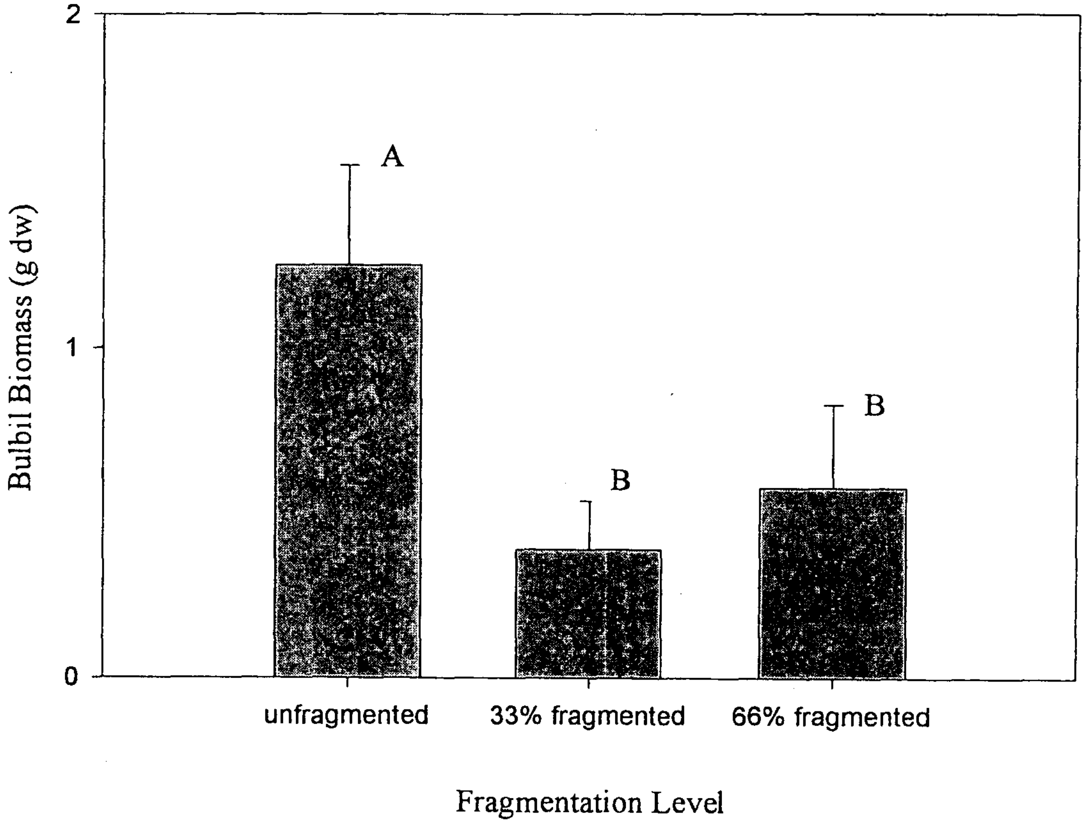


Figure 28. Number of bulbils produced by fertilized and unfertilized *D. oppopsitifolia* plants grown from whole bulbils, bulbils with 33% of their mass removed, or bulbils with 66% of their mass removed.

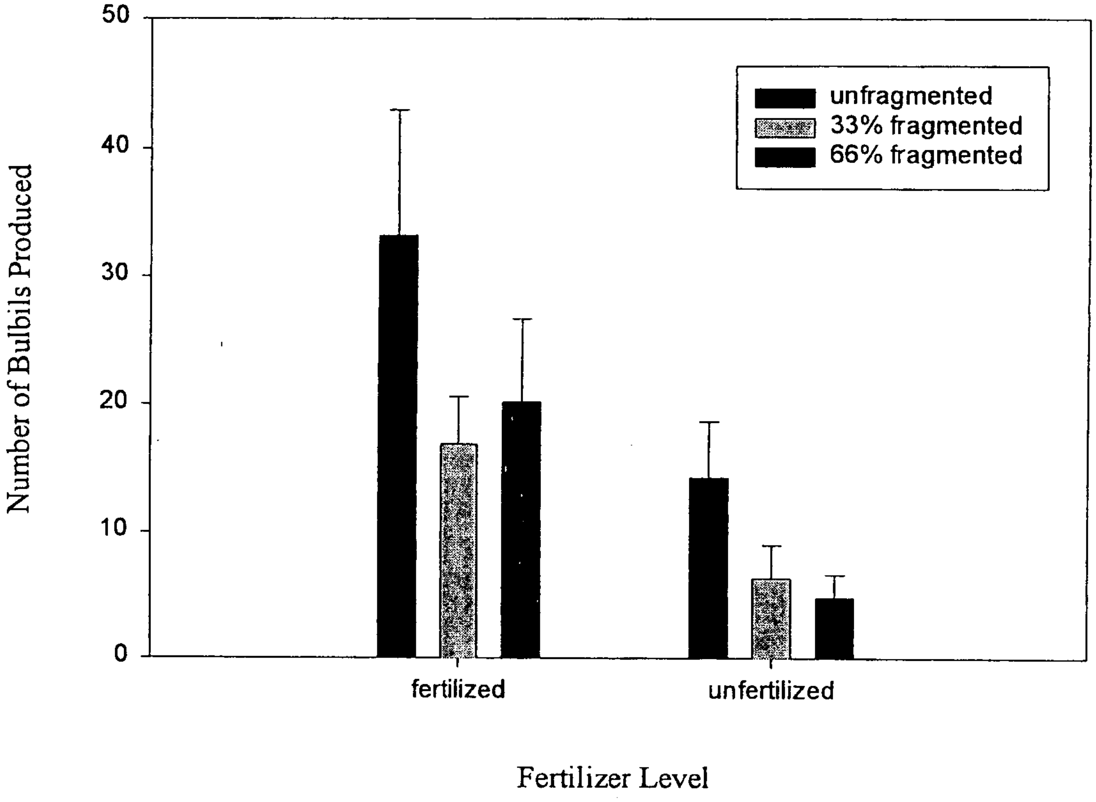


Figure 29. Number of bulbils germinating in glyphosate treated vs. untreated groups.

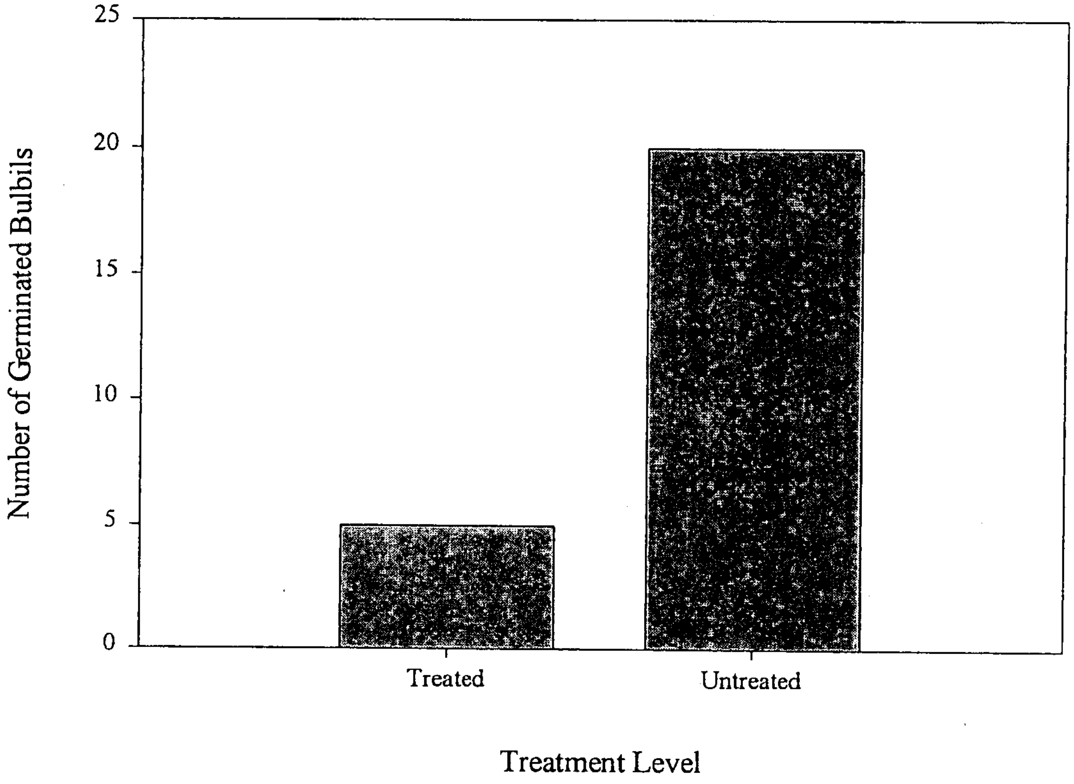


Figure 30. Mean stem length (+ 1 SE) of *D. oppositifolia* plants grown in the greenhouse from glyphosate treated vs. untreated bulbils.

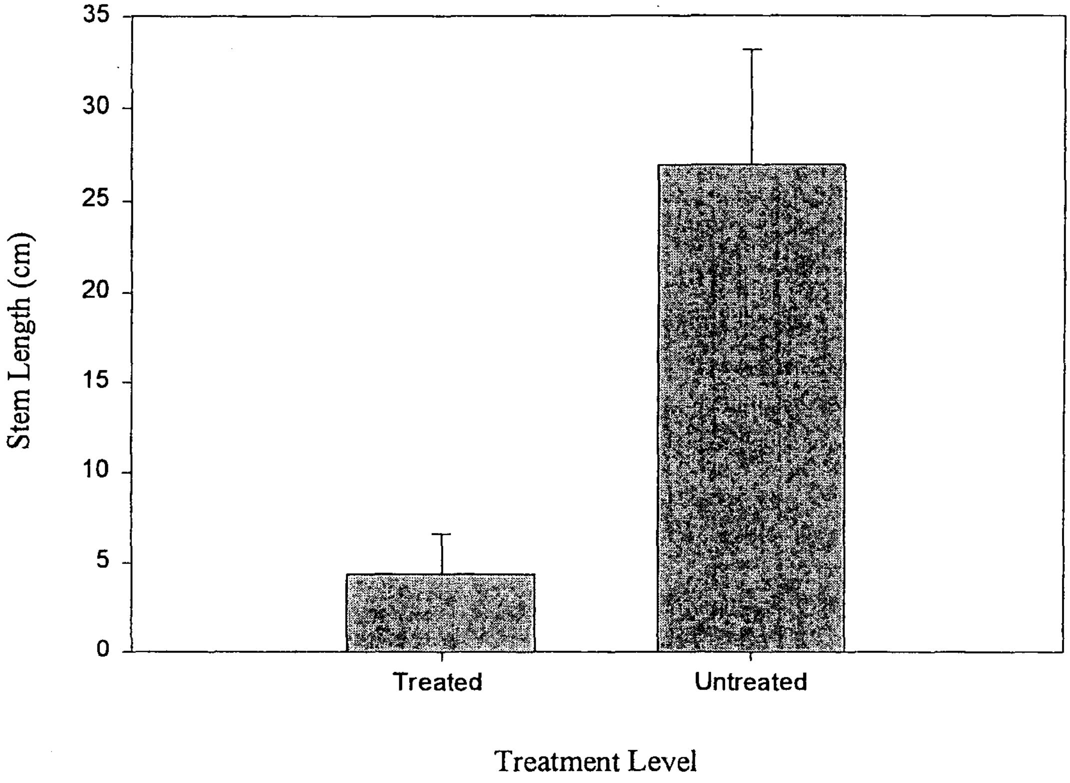
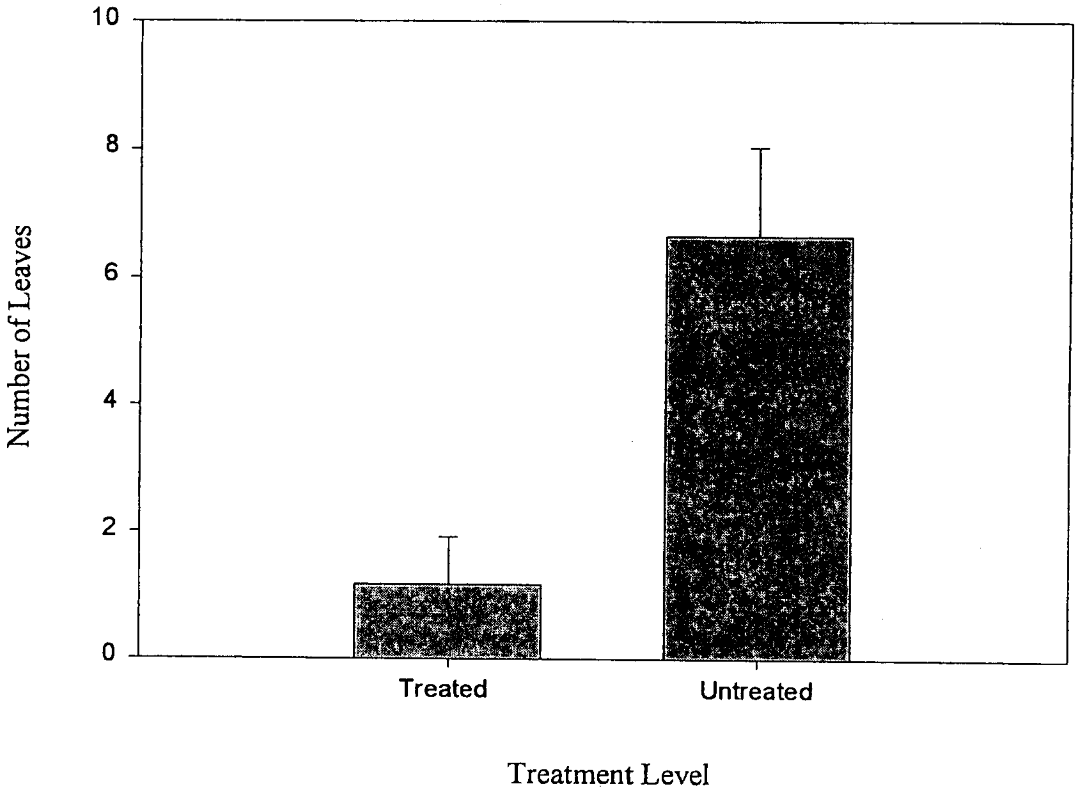


Figure 31. Number of leaves produced by *D. oppositifolia* plants grown from glyphosate treated vs. untreated bulbils.



LITERATURE CITED

Abrams, M and L Hulbert. 1987. Effect of topographic position and fire on species composition in a tallgrass prairie in northeast Kansas. *American MidlandNaturalist* 117: 442-445.

Armson, K.A. 1977. Forest Soils: Properties and Processes. University of Toronto Press, Toronto.

Baker, H.G. 1965. Characteristics and modes of origin of weeds. In: Baker, H.G. and G.L. Stebbins (eds). The Genetics of Colonizing Species. Academic Press, New York, pp. 147-172.

Baker, H.G. 1986. Patterns of plant invasion in North America. In: Mooney, H.A. and J.A. Drake (eds.). The Genetics of Colonizing Species. Academic Press, New York, NY pp. 57.

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

Bazzaz, F.A. 1986. Life history of colonizing plants. In: Mooney, H.A. and J.A. Drake (eds). Ecology of Biological Invasions of North America and Hawaii. Springer - Verlag, New York, NY pp. 96-108.

Brady, N.C 1974. The Nature and Properties of Soils. Eighth edition. Macmillan, New York.

Brandon, A.L. 2000. Effects of *Lespedeza cuneata*, an invasive species, on a successional old-field plant community. M.S. Thesis, Department of Plant Biology. Southern Illinois University, Carbondale, IL.

Bright, C. 2001. Invasive species: pathogens of globalization. In: Allen, J.L. (ed). Annual Editions Environment. McGraw-Hill Dushkin, CT.

Brown, V. K., A.C. Gange, I.M. Evans, and A.L. Storr. 1987. The effect of insect herbivory on the growth and reproduction of two annual *Vicia* species at different stages in plant succession. *Journal of Ecology* 75: 1173-1189.

Chambers, J.C. and J.A. MacMahon. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* 25: 263-292.

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

Coblentz, B. E. 1990. Exotic organisms: A dilemma for conservation biology. *Conservation Biology* 4: 261-265.

Cody, R.P. and J.K. Smith. 1997. Applied statistics and the SAS® programming language. Fourth Edition. Prentice-Hall, NJ.

Davis, M.A. and K. Thompson. 2000. Eight ways to be a colonizer; two ways to be an invader: A proposed nomenclature scheme for invasion ecology. *Bulletin of the Ecological Society of America* 81: 226-230.

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

Devine, R. 1998. Alien Invasion: America's Battle with Non-native Animals and Plants. The National Geographic Society, Washington D.C.

Dillenberg, L.R., D.F. Whigham, A.H. Teramura, and I.N. Forseth. 1993. Effects of below and above ground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*. *Oecologia* 93: 48-54.

Elsenheimer, T.E. 1994. The effect of 14 years of biennial spring burning on above ground biomass and woody plant invasion in four Alexander County, Illinois hill prairies. M.S. Thesis, Department of Plant Biology. Southern Illinois University, Carbondale, IL.

Gange, A.C., V.K. Brown, I.M. Evans, and A.L. Storr. 1989. Variation in the impact of insect herbivory on *Trifolium pratense* through early plant succession. *Journal of Ecology* 77: 537-551.

Gleason, H.A. and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Second edition. New York Botanical Garden, Bronx, NY.

Gordon, D.R. 1998. Effects of invasive, nonindigenous plant species on ecosystem processes: Lessons from Florida. *Ecological Applications* 8: 975-989.

Gould A.M.A. and D.L. Gorchov. 1998. Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. *American Midland Naturalist* 144: 36-50.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Midland Naturalist* 111: 1169-1195.

Groves, R.H. and J.J. Burdon. 1986. Ecology of Biological Invasions. Cambridge University Press, New York, NY.

Halvey, P. 1979. Thompson Woods serves SIU as environmental time capsule. The Daily Egyptian Vol. 73. March 6, 1979. Southern Illinois University Carbondale.

Hawley, W.O. 1956. Dioscoreas as ornamental foliage plants. *Natural Horticulture Magazine* 35(1): 23-29.

Henry, R.D. and A.R. Scott. 1981. Time of introduction of the alien component of the spontaneous Illinois vascular flora. *American Midland Naturalist* 106: 318-324.

Herman, R.J. 1979. Soil survey of Jackson County, Illinois. United States Department of Agriculture, Soil Conservation Service and Forest Service in cooperation with Illinois Agricultural Experiment Station. US Government Printing Office, Washington D.C.

Illinois Department of Energy and Natural Resources. 1994. The Changing Illinois Environment: Critical Trends. Summary Report and Volumes 1-7 Technical Report. Illinois Department of Energy and Natural Resources, Springfield, IL.

Lockhart, C.S., D.F. Austin, W.E. Jones, and L.A. Downey. 1999. Invasion of carrotwood (*Cupaniopsis anacardioides*) in Florida Natural Areas (USA). *Natural Areas Journal* 19: 254-262.

Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80: 1522-1536.

Mabberly, D.J. 1989. The Plant Book. A Portable Dictionary of the Higher Plants. Cambridge University Press, New York, NY.

Melgoza, G., R.S. Nowak, and R.J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83: 7-13.

Marone, L., M.E. Horno, and R.G.D. Solar. 2000. Post-dispersal fate of seeds in the Monte desert of Argentina: pattern of germination in successive wet and dry years. *Journal of Ecology* 88: 940-949.

McCarthy, J.R. 1995. Above and below-ground tree growth of a 1981 reforestation planting on a reclaimed minesoil in southern Illinois. M.S. Thesis, Department of Plant Biology. Southern Illinois University, Carbondale, IL.

McCune, B. and M.J. Mefford. 1999. PC-ORD for Windows. Multivariate Analysis of Ecological Data. Version 4.0. MjM Software, Glenden Beach, OR.

Mohlenbrock, R.H. 1970. The Illustrated Flora of Southern Illinois. *Flowering Plants: Lilies to Orchids.* Southern Illinois University Press, Carbondale, IL.

______. 1986. Guide to the Vascular Flora of Southern Illinois. Revised and Enlarged Edition. Southern Illinois University Press, Carbondale, IL.

Mun, H.T., , M.S. Nam, and S.R.Cho. 1996. Changes of forest soil and herb layer composition by group breeding of herons. *Journal of the Korean Forestry Society* 85: 506-512.

Myster, R.W. and S.T.A. Pickett. 1992. Dynamics of associations between plants in ten old fields during 31 years of succession. *Journal of Ecology* 80: 291-302.

National Biological Information Infrastructure. 2000. *Invasive Species.* United States Geological Survey. [Online]. Accessed: January, 2000. Available: http://www.nbii.gov/invasive/

Neufeldt, V. and D.B. Guralnik (eds.). 1988. Webster's New World Dictionaryof American English. Simon and Schuster, New York, NY.

Parks, W.D. 1975. Soil survey of Pope, Hardin, and Massac Counties, Illinois. United States Department of Agriculture, Soil Conservation Service and Forest Service in cooperation with Illinois Agricultural Experiment Station. US Government Printing Office, Washington D.C.

PCA (Plant Conservation Alliance). 2000. Alien Plant Working Group. Bureau of Land Management. [Online]. Accessed: January, 2000. Available: http://www.nps.gov/plants/alien

Plants for a Future. 1999. [Online]. Accessed: January, 2000. Available: http://www.scs.leeds.ac.uk/pfaf/D_intro.html

Rejmanek, M., and J. Randall. 1994. Invasive alien plants in California: 1993 summary and comparison with other areas in North America. *Madrono* 41(3):161-177.

SAS Institute. 1999. The SAS System for Windows. Version 8.00. The SAS Institute, Cary, NC.

Schultz, K. and C. Thelen. 2000. Impact and control of *Vinca minor* L. in an Illinois forest preserve (USA). *Natural Areas Journal* 20: 189-196.

Schmitz, D.C. and T.C. Brown (eds.). 1994. An assessment of invasive, non-indigenous species in Florida's public lands. Technical Report No. TSS-94-100, Florida Department of Environmental Protection, Bureau of Aquatic Plant Management, Tallahassee, FL.

Simberloff, D., D.C. Schmitz, and T.C. Brown. 1997. Strangers in Paradise: Impact and Management of Non-indigenous Species in Florida. Island Press, Washington D.C.

Silvertown, J.W. and J. Lovett Doust. 1993. Introduction to Plant Population Biology. Third Edition. Blackwell Science, Oxford.

The Nature Conservancy. 2000. *Weeds on the Web*. Wildland Invasive Species Program. [Online]. Accessed: January, 2000. Available: http://tncweeds.ucdavis.edu/tncweeds.html

Tilman, D. and D. Wedin. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

USDA, National Resource Conservation Service 2001. The PLANTS database. [Online]. Accessed: February, 2000. Available: (http://plants.usda.gov/plants). National Plant Data Center, Baton Rouge, LA.

van Groenendael, J. M. and P. Slim. 1988. The contrasting dynamics of two populations of *Plantago lanceolata* classified by age and size. *Journal of Ecology* 76: 585-599.

Vitousek, P.M., C.M. D'Antonio, L.L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84: 468-478.

Wallace, D.L. and J.B. Fehrenbacher. 1967. Soil survey of Gallatin County, Illinois. United States Department of Agriculture, Soil Conservation Service and Forest Service in cooperation with Illinois Agricultural Experiment Station. US Government Printing Office, Washington D.C.

Waller, D.M. 1986. The dynamics of growth and form. In: M.J. Crawley (ed.). Plant Ecology. Blackwell Scientific Publications, Oxford, pp. 291-320

Welch, B. L. 1938. The significance of the difference between two means when the population variances are unequal. *Biometrika* 29: 350-361. [Cited in Zar (1999).]

White, J. and M.H. Madany. 1978. Classification of Natural Communities in Illinois. In: J. White, editor, Illinois Natural Area Inventory and Technical Report, volume 1, Survey methods and results. Illinois Department of Conservation, Springfield, Appendix 30, pp. 309-405.

Williamson, M. 1996. Biological Invasions. Chapman and Hall, London.

Woods, K.D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. *American Midland Naturalist* 130: 62-74.

Yatskievych, G. 1999. Steyermark's Flora of Missouri Volume 1. Missouri Department of Conservation, Jefferson City, MO in association with the Missouri Botanical Garden Press, St. Louis, MO.

Young, J.L. and R.W. Aldag. 1982. Inorganic forms of nitrogen in soil. In: F. J. Stevenson (ed.). Nitrogen in Agricultural Soils. American Society of Agronomy, Madison, WI, pp. 43-66.

Zar, J.H. 1996. Biostatistical Analysis. Third Edition. Prentice Hall, Upper Saddle River, NJ.

Zomlefer, W.B. 1994. Guide to Flowering Plant Families. The University of North Carolina Press, Chapel Hill, NC.

APPENDICES

APPENDIX 1

List of species growing in association with *Dioscorea oppositifolia* at the Douglas Dr. site. Nomenclature according to Gleason and Cronquist (1991).

Scientific Name	Species Code
**Euonymus fortunei*	EUFO
**Festuca elatior*	FEAR
**Glechoma hederacea*	GLHE
**Lonicera japonica*	LOJA
**Lonicera maackii*	LOMA
**Ranunculus parviflorus*	RAPA
**Rosa multiflora*	ROMU
Acer negundo	ACNE
Acer saccharum	ACSA
Aesculus pavia	AEPA
Albizzia julibrissin	ALJU
Amphicarpa bracteata	AMBR
Asimina triloba	ASTR
Campsis radicans	CARA
Cassia nicitans	CANI
Cornus drummondii	CODR
Desmodium canescens	DECA
Elymus villosus	ELVI
Erigeron philadelphicus	ERPH
Eupatorium rugosum	EURU
Fraxinus americana	FRAM
Geum canadense	GECA
Impatiens capensis	IMCA
Panicum dichotomiflorum	PADI
Parthenocissus quinquefolia	PAQU
Podophyllum peltatum	POPE
Prunus serotina	PRSE
Sanicula canadensis	SANCA
Solidago canadensis	SOCA
Toxicodendron radicans	TORA
Trillium recurvatum	TRRE
Vitis vulpina	VIVU

*Exotic Species

APPENDIX 2

List of species growing in association with _Dioscorea oppositifolia_ at the Thompson Woods sites. Nomenclature according to Gleason and Cronquist (1991).

Thompson Woods I		Thompson Woods II	
Scientific Name	Species Code	Scientific Name	Species Code
*_Euonymus alata_	EUAL	*_Euonymus alata_	EUAL
*_Euonymus fortunei_	EUFO	*_Euonymus fortunei_	EUFO
*_Lonicera japonica_	LOJA	*_Lonicera maackii_	LOMA
*_Lonicera maackii_	LOMA	_Acer negundo_	ACNE
*_Narcissus pseudo-narcissus_	NAPS	_Acer saccharum_	ACSA
*_Urtica dioica_	URDI	_Aesculus pavia_	AEPA
Acer saccharinum	ACSAI	_Arum italicum_	ARIT
Acer saccharum	ACSA	_Celtis occidentalis_	CEOC
Aesculus pavia	AEPA	_Cercis canadensis_	CECA
Asimina triloba	ASTR	_Cornus florida_	COFL
Boehmeria cylindrica	BOCY	_Fraxinus americana_	FRAM
Campsis radicans	CARA	_Galium aparine_	GAAP
Carpinus caroliniana	CACA	_Liriodendron tulipifera_	LITU
Celtis occidentalis	CEOC	_Parthenocissus quinquefolia_	PAQU
Cornus florida	COFL	_Quercus imbricaria_	QUIM
Corydalis flavula	COFLV	_Quercus palustris_	QUPA
Corylus americana	COAM	_Quercus velutina_	QUVE
Elymus villosus	ELVI	_Sambucus canadensis_	SAMCA
Eupatorium rugosum	EURU	_Sanicula canadensis_	SANCA
Fraxinus americana	FRAM	_Sassafras albidum_	SAAL
Geum canadense	GECA	_Toxicodendron radicans_	TORA
Lactuca floridana	LAFL	_Tsuga canadensis_	TSCA
Liriodendron tulipifera	LITU	_Vitis cinerea_	VICI
Morus alba	MOAL		
Parthenocissus quinquefolia	PAQU		
Platanus occidentalis	PLOC		
Prunus serotina	PRSE		
Robinia pseudoacacia	ROPS		
Rubus pensilvanicus	RUPE		
Sambucus canadensis	SAMCA		
Sanicula canadensis	SANCA		
Sassafras albidum	SAAL		
Ulmus rubra	ULRU		
Viburnum recognitum	VIRE		
Viola sororia	VISO		
Vitis cinerea	VICI		

*Exotic Species

APPENDIX 3

List of species growing in association with *Dioscorea oppositifolia* at the Landreth Rd. sites. Nomenclature according to Gleason and Cronquist (1991).

Landreth I		Landreth II	
Scientific Name	Species Code		Species Code
**Allium vineale*	ALVI	**Allium vineale*	ALVI
**Festuca elatior*	FEAR	**Cirsium vulgare*	CIVU
**Lonicera japonica*	LOJA	**Eragrostis curvula*	ERCU
**Lonicera maackii*	LOMA	**Festuca elatior*	FEAR
**Plantago major*	PLMA	**Lamium amplexicaule*	LAAM
**Rosa multiflora*	ROMU	**Lonicera japonica*	LOJA
**Sorghum halepense*	SOHA	**Plantago lanceolata*	PLLA
**Trifolium repens*	TRRE	**Polygonum cespitosum*	POCE
Acer negundo	ACNE	**Rosa multiflora*	ROMU
Acer nigra	ACNI	**Rumex crispus*	RUCR
Acer saccharum	ACSA	**Stellaria media*	STME
Allium canadense	ALCA	**Trifolium repens*	TRRE
Amphicarpa bracteata	AMBR	**Urtica dioica*	URDI
Botrychium virginianum	BOVI	*Acer negundo*	ACNE
Campsis radicans	CARA	*Acer rubrum*	ACRU
Celtis laevigata	CELA	*Acer saccharum*	ACSA
Cercis canadensis	CECA	*Ambrosia trifida*	AMTR
Desmodium canescens	DECA	*Asclepias tuberosa*	ASTU
Elymus hystrix	ELHY	*Celtis laevigata*	CELA
Elymus virginicus	ELVI	*Elymus virginicus*	ELVI
Erigeron annuus	ERAN	*Eupatorium rugosum*	EURU
Eupatorium rugosum	EURU	*Fraxinus americana*	FRAM
Fraxinus americana	FRAM	*Geum canadense*	GECA
Galium triflorum	GATR	*Parthenocissus quinquefolia*	PAQU
Geum canadense	GECA	*Phaseolus polystachios*	PHPO
Iris virginica Var. shrevei	IRPR	*Polygonum scandens*	POSC
Juglans nigra	JUNI	*Potentilla simplex*	POSI
Panicum anceps	PAAN	*Rhus glabra*	RHGL
Panicum dichotomiflorum	PADI	*Rubus pensilvanicus*	RUPE
Parthenocissus quinquefolia	PAQU	*Rubus occidentalis*	RUOC
Phaseolus polystachios	PHPO	*Salix nigra*	SANI
Prunus serotina	PRSE	*Sambucus canadensis*	SAMCA
Rhus glabra	RHGL	*Solidago canadensis*	SOCA
Rubus pensilvanicus	RUPE	*Solidago rugosa*	SORU
Sambucus canadensis	SAMCA	*Toxicodendron radicans*	TORA
Sassafras albidum	SAAL	*Ulmus americana*	ULAM
Smilax hispida	SMHI	*Ulmus rubra*	ULRU

Solidago canadensis	SOCA	*Verbena urticifolia*	VEUR
Toxicodendron radicans	TORA	*Viola pratincola*	VIPR
Trillium recurvatum	TRRE	*Vitis spp.*	VITIS
Ulmus rubra	ULRU		
Vernonia missurica	VEMI		
Viola spp.	VIOLA		
Vitis spp.	VITIS		

*Exotic Species

APPENDIX 4

List of species growing in association with *Dioscorea oppositifolia* at the York Ln. site. Nomenclature according to Gleason and Cronquist (1991).

Scientific Name	Species Code		Species Code
**Festuca elatior*	FEAR	*Galium aparine*	GAAP
**Lonicera japonica*	LOJA	*Geum canadense*	GECA
**Melilotus officinalis*	MEOF	*Liquidambar styraciflua*	LIST
**Microstegium vimineum*	MIVI	*Liriodendron tulipifera*	LITU
**Plantago rugellii*	PLRU	*Morus alba*	MOAL
**Poa pratensis*	POPR	*Panicum boscii*	PABO
**Polygonum cespitosum*	POCE	*Parthenocissus quinquefolia*	PAQU
**Prunella vulgaris*	PRSE	*Phytolacca americana*	PHAM
**Rosa multiflora*	ROMU	*Pinus strobus*	PIST
**Trifolium pratense*	TRPR	*Polygonum scandens*	POSC
**Viola rafinesquii*	VIRA	*Quercus marilandica*	QUMA
Acer rubrum	ACRU	*Rhus glabra*	RHGL
Acer saccharum	ACSA	*Robinia pseudoacacia*	ROPS
Ambrosia artemisiifolia	AMBR	*Rubus occidentalis*	RUOC
Ambrosia trifida	AMTR	*Rubus pensilvanicus*	RUPE
Apocynum cannabinum	APCA	*Sassafras albidum*	SAAL
Asclepias syriaca	ASSY	*Senecio aureus*	SEAU
Asplenium platyneuron	ASPL	*Solidago canadensis*	SOCA
Bidens aristosa	BIAR	*Toxicodendron radicans*	TORA
Boehmeria cylindrica	BOCY	*Ulmus alata*	ULAL
Celtis occidentalis	CEOC	*Ulmus americana*	ULAM
Cornus florida	COFL	*Verbascum thapsus*	VETH
Desmondium canescens	DECA	*Verbena urticifolia*	VEUR
Eupatorium coelestinum	EUCO	*Vitis spp.*	VITIS
Eupatorium rugosum	EURU		
Fraxinus americana	FRAM		

*Exotic Species

APPENDIX 5

List of species growing in association with *Dioscorea oppositifolia* at the Lusk Creek Natural Area site. Nomenclature according to Gleason and Cronquist (1991).

Scientific Name	Species Code	Scientific Name	Species Code
**Commelina communis*	COCO	*Leersia oryzoides*	LEOR
**Digitaria ischaemum*	DIIS	*Leersia virginica*	LEVI
**Microstegium vimineum*	MIVI	*Lindera benzoin*	LIBE
**Rosa multiflora*	ROMU	*Liquidambar styraciflua*	LIST
**Stellaria media*	STME	*Liriodendron tulipifera*	LITU
**Trifolium pratense*	TRPR	*Ostrya virginiana*	OSVI
Acer rubrum	ACRU	*Oxalis stricta*	OXST
Agrostis perennans	AGPE	*Parthenocissus quinquefolia*	PAQU
Andropogon gerardii	ANGE	*Perilla frutescens*	PEFR
Asimina triloba	ASTR	*Phlox divaricata*	PHDI
Aster simplex	ASSI	*Phytolacca americana*	PHAM
Barbarea vulgaris	BAVU	*Platanus occidentalis*	PLOC
Betula nigra	BENI	*Polemonium reptans*	PORE
Boehmeria cylindrica	BOCY	*Polygonatum commutatum*	POCO
Botrychium virginianum	BOVI	*Polygonum pennsylvanicum*	POPE
Campsis radicans	CARA	*Polygonum sagittatum*	POSA
Carpinus caroliniana	CACA	*Polygonum scandens*	POSC
Carya glabra	CAGA	*Polystichum acrostichoides*	POAC
Carya tomentosa	CATO	*Potentilla simplex*	POSI
Chasmanthium latifolium	CHLA	*Prunella vulgaris*	PRVU
Conyza canadensis	COCA	*Prunus serotina*	PRSE
Corydalis flavula	COFL	*Quercus alba*	QUAL
Corylus americana	COAM	*Quercus muhlenbergii*	QUMU
Desmodium canescens	DECA	*Quercus palustris*	QUPA
Desmodium paniculatum	DEPA	*Quercus velutina*	QUVE
Dicentra cucullaria	DICU	*Rudbeckia laciniata*	RULA
Diospyros virginiana	DIVI	*Sambucus canadensis*	SAMCA
Elephantopus carolinianus	ELCA	*Sanicula canadensis*	SANCA
Erigeron annuus	ERAN	*Senecio aureus*	SEAU
Eupatorium purpureum	EUPU	*Smilax hispida*	SMHI
Eupatorium rugosum	EURU	*Smilax lasioneuron*	SMLA
Fraxinus pennsylvanica	FRAM	*Solidago canadensis*	SOCA
Geranium maculatum	GEMA	*Toxicodendron radicans*	TORA
Geum canadense	GECA	*Tradescantia virginiana*	TRVI
Hydrangea arborescens	HYAR	*Ulmus rubra*	ULRU
Hydrophyllum appendiculatum	HYAP	*Verbesina alternifolia*	VEAL
Impatiens capensis	IMCA	*Vitis* spp.	VITIS

APPENDIX 6

List of species growing in association with *Dioscorea oppositifolia* at the Lamb Rd. site. Nomenclature according to Gleason and Cronquist (1991).

Scientific Name	Species Code	Scientific Name	Species Code
*_Allium vineale_	ALVI	_Elymus villosus_	ELVI
*_Barbarea vulgaris_	BAVU	_Elymus virginicus_	ELVIR
*_Cardamine hirsuta_	CAHI	_Erigeron philidelphicus_	ERPH
*_Daucus carota_	DACA	_Erythronium americanum_	ERAM
*_Festuca elatior_	FEAR	_Galium aparine_	GAAP
*_Lamium pupureum_	LAPU	_Geranium carolinianum_	GECAR
*_Lonicera japonica_	LOJA	_Geranium maculatum_	GEMA
*_Microstegium vimineum_	MIVI	_Geum canadense_	GECA
*_Poa pratensis_	POPR	_Impatiens capensis_	IMCA
*_Rumex obtusifolius_	RUOB	_Isopyrum biternatum_	ISBI
*_Stellaria media_	STME	_Lactuca floridana_	LAFL
*_Taraxacum officinale_	TAOF	_Lindera benzoin_	LIBE
*_Trifolium pratense_	TRPR	_Osmorhiza longistylis_	OSLO
*_Verbascum thapsus_	VETH	_Oxalis dillenii_	OXDI
*_Vinca minor_	VIMI	_Perilla frutescens_	PEFR
Ulmus americana	ULAM	_Phlox paniculata_	PHPA
Acer negundo	ACNE	_Podophyllum peltatum_	POPEL
Allium canadense	ALCA	_Polemonium reptans_	PORE
Ambrosia artemisiifolia	AMAR	_Polygonatum commutatum_	POCO
Ambrosia trifida	AMTR	_Polygonum virginianum_	POVI
Aster drummondii	ASDR	_Rudbeckia triloba_	RUTR
Aster simplex	ASSI	_Sambucus canadensis_	SAMCA
Blephilia hirsuta	BLHI	_Sanguinaria canadensis_	SAGCA
Campanula americana	CAAM	_Scrophularia marilandica_	SCMA
Chaerophyllum tainturieri	CHTA	_Senecio aureus_	SEAU
Claytonia virginica	CLVI	_Solidago canadensis_	SOCA
Corydalis flavula	COFL	_Symphoricarpos orbiculatus_	SYOR
Cryptotaenia canadensis	CRCA	_Tridens flavus_	TRFL
Cystopteris protrusa	CYPR	_Trillium recurvatum_	TRRE
Delphinium tricorne	DETR	_Verbena urticifolia_	VEUR
Dentaria laciniata	DELA	_Viola pubescens_	VIPU
Dicentra cucullaria	DICU	_Viola sororia_	VISO
Elephantopus carolinianus	ELCA		

* Exotic Species

VITA

Graduate School
Southern Illinois University

Tammie Beyerl Date of Birth: March 16, 1967

1716 Westmeade Dr., Chesterfield, Missouri 63017

Truckee Meadows Community College
General Studies

University of Nevada – Reno
Conservation Biology

Southern Illinois University at Carbondale
Bachelor of Arts Plant Biology (1999)

Honors and Awards:
Dean's List two semesters, SIUC Department of Science
Junior Class Scholastic Honors Award, SIUC
Senior Class Scholastic Honors Award, SIUC
John W. Voigt Natural History of Plants Award
Graduated Cum Laude
Poster presentation award from the Society of Wetland Scientists, Southeastern Region

Grants:
Illinois Department of Natural Resources Natural Heritage Grant ($1000.00)

Thesis Title:

Habitat and life history characteristics of *Dioscorea oppositifolia*, an invasive plant species in southern Illinois.

Major Professor: David J. Gibson

Publications:

Beyerl, T.R. and D.J. Gibson. 2001. Habitat and life history characteristics of *Dioscorea oppositifolia* L., an invasive plant species in southern Illinois. Southeastern Biology, 48 (2), pp 146.

Hoyer, E.W, T.R. Beyerl, M. Minzner, L. Brennan, and B.A. Middleton. 2001. Functional analysis of planted, regenerated, and old-growth cypress wetlands along the Cache River, Illinois. Southeastern Biology 48 (2), pp 107.

Hoyer, E.W, T.R. Beyerl, M. Minzner, L. Brennan, and B.A. Middleton. 2001. Functional analysis of planted, regenerated, and old-growth cypress wetlands along the Cache River, Illinois. The Ecological Society of America 86th Annual Meeting Abstracts pp. 295.