ECOLOGY OF *RUDBECKIA AURICULATA* (PERDUE) KRAL (ASTERACEAE)

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ECOLOGY OF *RUDBECKIA AURICULATA* (PERDUE) KRAL (ASTERACEAE)

Alvin R. Diamond, Jr.

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ECOLOGY OF *RUDBECKIA AURICULATA* (PERDUE) KRAL (ASTERACEAE)

Alvin R. Diamond, Jr.

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VITA

Alvin Roosevelt Diamond Jr., son of Alvin R. Diamond Sr. and Ina (Etheridge) Diamond, was born August 12, 1962, in Evergreen, Alabama. He graduated from Evergreen High School in 1980. He attended Jefferson Davis Junior College in Brewton, Alabama, for two years and graduated in June of 1982 with an Associates of Arts degree. He then entered Troy University in September, 1982, and graduated with a Bachelor of Science degree in Biology in June, 1984. In September of 1984 he entered Graduate School in Auburn University's Department of Botany, Plant Pathology, and Microbiology, earning his Master of Science degree in August of 1987. After working as Director of the Troy University Arboretum for ten years, he entered Graduate School, Auburn University, in September, 1998.

DISSERTATION ABSTRACT

ECOLOGY OF *RUDBECKIA AURICULATA* (PERDUE) KRAL (ASTERACEAE)

Alvin R. Diamond, Jr.

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(A.A., Jefferson Davis College, 1982)

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Rudbeckia auriculata is a rare species endemic to three southeastern states: Alabama, Florida, and Georgia. Eight censuses of flowering individuals of the species were conducted from 1992 to 2002. Although the number of known populations increased during the census period, total counts of flowering stems remained relatively constant. Population sizes ranged from one individual with a single flowering stem to populations with over 1,000 flowering stems. Information on soils and associated species of vascular plants was collected at twenty of the thirty-two known sites. Typical sites are on wet soils along roadsides, power line right-of-ways or are otherwise disturbed. Associated species are characteristic of disturbed open wetland sites. Although some large colonies of *R. auriculata* still exist, only two populations, both in the northern portion of the species' range, have been protected.

Observations of insect abundance on flower heads and analysis of pollen loads on floral visitors indicated that the most likely pollinators are *Andrena aliciae* Robertson (in medium and large *Rudbeckia auriculata* populations) and Halictids (in small populations). Achene set varied from 0.24% to 16.9% in small populations (< 40 flowering stems) and from 26.5% to 31.4% in medium (40-999 flowering stems) and large (≥ 1000 flowering stems) populations. Achene set was significantly lower in the small populations. Exclusion of visitors from inflorescences showed that *R. auriculata* is probably self-incompatible and thus requires insect vectors for successful pollination and achene set. Achene dispersal appears to be highly localized and dependent upon gravity. Seedling recruitment is poor.

The fungus *Fusarium semitectum* Berk. & Ravenel infects the flowering heads of *Rudbeckia auriculata* at two sites in Alabama. The fungus produces orangish or pinkish-white spores on the flower heads and renders infected flowers sterile. Fungal spores superficially resembled pollen and are picked up by the main pollinator, the composite specialist bee *Andrena aliciae*, which serves as a dispersal agent for the fungal pathogen. The fungus appears to pose no serious threat to the species at this time.

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TABLE OF CONTENTS

LIST OF TABLES AND FIGURES

IV FIGURES

IV TABLES

I. INTRODUCTION

Rudbeckia auriculata (Perdue) Kral (Asteraceae) is a rare wetland plant native to the southeastern United States. The majority of known populations occur in Alabama (30 of 32), with one known population extant in Georgia and one historical population in Florida (Diamond and Boyd 2004, Schotz 2000, Diamond and Owens 1993, Diamond 1992, Kral 1983, McDaniel 1981) (Fig. 1). Of this number, six have been extirpated within the past 20 years. Although a few of the remaining sites support over 1,000 flowering stems, 19 support 50 or fewer flowering stems (Diamond and Boyd 2004, Schotz 2000).

In Alabama, the species is known from Barbour, Bullock, Covington, Crenshaw, Pike and Geneva counties in the southeastern portion of the state and Blount, Jefferson, St. Clair, and Shelby counties in the north-central part of the state. In Georgia, it is known from Webster County in the southwestern part of the state, and is apparently extirpated from Walton County, Florida. *Rudbeckia auriculata* is listed as critically imperiled globally, and critically imperiled within their states by both the Alabama and Georgia Natural Heritage Programs (Alabama Natural Heritage Program 2004, Georgia Natural Heritage Program 2004).

Rudbeckia auriculata was first collected by R. E. Perdue on July 24th of 1958 near Red Level in Covington County, Alabama, and described as variety *auriculata* of

Rudbeckia fulgida Aiton, a species in subgenus *Rudbeckia* (Perdue 1961). The type specimen is Perdue 2177: Covington County, Alabama: Along Alabama Hwy. 55, 11 miles south of McKenzie, 2 miles north of Red Level, 24 July 1958 (holotype GH; isotype US). Kral (1975) subsequently raised the variety to species rank, and suggested a closer affinity of *R. auriculata* to *Rudbeckia nitida* Nutt. and *Rudbeckia mohrii* A. Gray, species now placed in subgenus *Macrocline.* In a taxonomic revision of the subgenus *Macrocline*, Cox and Urbatsch (1994) stated that *R. auriculata* has morphological and habitat similarities to the east Texas and west Louisiana endemic *Rudbeckia scabrifolia* L.E. Brown, but is probably more closely related to the southeastern coastal plain species *Rudbeckia nitida* and *Rudbeckia mohrii*. Chloroplast DNA evidence and internal transcribed spacer (ITS) sequence data support a close relationship between *R. auriculata* and *R. scabrifolia* (Urbatsch *et al.* 2000, Urbatsch and Jansen 1995). Spontaneous garden hybrids between *R. auriculata* and *R. laciniata* L. have been reported (Urbatsch *et al.* 2001).

Rudbeckia auriculata is perennial and clonal, a life form that is prevalent throughout southeastern wetlands (Edwards and Weakley 2001). Vegetative rosettes of large (to 6.5 dm) oblong to oblanceolate evergreen basal leaves are produced. Under favorable conditions each rosette produces one or more flowering stems up to 3 meters in height, with numerous auriculate clasping leaves (Fig. 2). Stems are terete or slightly ribbed. This combination of characteristics makes *R. auriculata* morphologically distinct in its genus. The genus *Rudbeckia* is a member of the composite tribe Heliantheae (Cronquist 1980), which is characterized by the presence of sticky masses of pollen presented at the anther tips that are rarely disturbed by either shaking or wind (Dickinson and McKone 1992). *Rudbeckia auriculata* heads are in numerous, open panicles, and are approximately 5.5 cm broad with an average of 12 bright orange-yellow ray flowers. Disc flowers are conical and purplish-black. Disc flowers open in the early morning, and the bright yellow pollen is easily visible against the purplish-black color of the head. Receptive stigmas in the Heliantheae are located near the disc, in a position easily contacted by insects (Dickinson and McKone 1992). Despite being conspicuous members of the flora, little information exists on the floral visitors of members of this tribe (Dickinson and McKone 1992). The flowering period for *R. auriculata* is late July through early November, although most plants are finished by September. Achenes usually are mature in October. The fruit is a purplish-brown achene approximately 4.0 - 4.5 mm in length with four to six teeth up to 2 mm long at its apex (Kral 1983, 1975; Schotz 2000). Dispersal is gradual over a period of several months as the head slowly breaks apart.

Since its discovery, three status surveys have been conducted on *R. auriculata* for the U.S. Fish and Wildlife Service (Schotz 2000, Diamond 1992, McDaniel 1981) as well as one technical report for the U.S. Forest Service (Kral 1983). Two of the reports to the U.S. Fish and Wildlife Service, those of Schotz (2000) and Diamond (1992), recommended that the species receive formal protection under the Endangered Species Act. Taxonomic keys including this species can be found in *Vascular Flora of the southeastern United States- vol. 1 Asteraceae* (Cronquist 1980), and *Aquatic and Wetland Plants of the southeastern United States: Dicotyledons* (Godfrey and Wooten 1981). Photographs are available online at Alvin Diamond's homepage (http://spectrum.troy.edu/~diamond/pikepics/Rudbeckia%20auriculata.JPG), Blackwarrior Riverkeeper (http://www.blackwarriorriver.org/coneflower.htm), and the University of South Florida's Institute for Systematic Botany (http://www.plantatlas.usf.edu/images.asp?plantID=4103#).

The southeastern region of the United States has long been recognized as an area of high biological diversity, containing many endemic plant species (Estill and Cruzan 2001, Ricketts *et al.* 1999, Flather *et al.* 1998, Dobson *et al.* 1997, Gentry 1986, Kral 1983). The Atlantic and Gulf Coastal Plain Floristic Province ranks second in the number of endemic species of floristic regions in North America north of Mexico (Sorrie and Weakley 2001). Many of these endemics are also rare within the region, making them vulnerable to extinction (Estill and Cruzan 2001). One such species is *R. auriculata*. The general rarity of *R. auriculata*, but local abundance at certain sites, suggests that one or more factors limit population size and dispersal of this species. However, extensive surveys have failed to document substantial numbers of new populations (Diamond and Boyd 2004, Schotz 2000, Diamond and Owens 1993, Diamond 1992, Kral 1983, McDaniel 1981). Among possible factors limiting population size and spread of this species are lack of pollinators, poor achene set, poor achene dispersal, low germination rates, and poor seedling recruitment (Schotz 2000).

This research was designed to provide information on: (1) the distribution, population trends, and associated soils and vegetation of *R. auriculata* populations; (2) potential pollinators, achene set, germination requirements, achene dispersal, and seedling recruitment of *R. auriculata*; and (3) fungal infection of *R. auriculata*, and the spread of the fungal pathogen. This study provides valuable information for the management of this species as well as base-line data for continued monitoring efforts.

Figure 1: Distribution by county of *Rudbeckia auriculata* (Perdue) Kral in the southeastern United States.

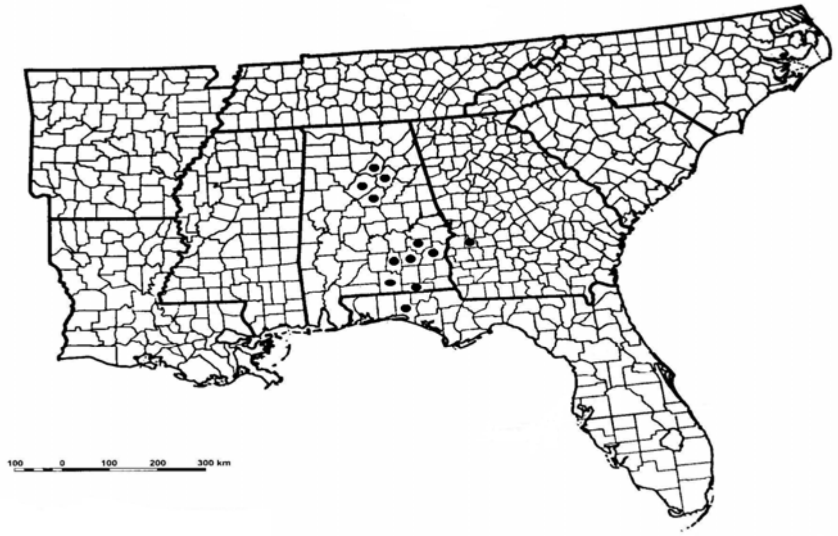

Figure 2: Auriculate-clasping stem leaves of *Rudbeckia auriculata.*

II. DISTRIBUTION, HABITAT CHARACTERISTICS, AND POPULATION TRENDS

INTRODUCTION

The southeastern region of the United States has long been recognized as an area of high biological diversity, containing many endemic plant species (Estill and Cruzan 2001, Ricketts *et al.* 1999, Flather *et al.* 1998, Dobson *et al.* 1997, Gentry 1986, Kral 1983). The Atlantic and Gulf Coastal Plain Floristic Province ranks second in the number of endemic species of floristic regions in North America north of Mexico (Sorrie and Weakley 2001). Many of these endemics are also rare within the region, making them vulnerable to extinction (Estill and Cruzan 2001). One such species is *Rudbeckia auriculata* (Perdue) Kral. Fiedler (1986) states that determining the distribution of a species can contribute to an understanding of the possible reasons for its rarity. This research provides additional information on the distribution, population trends, and associated soils and vegetation of *R. auriculata*.

METHODS

Distribution

Historical records were obtained for *R. auriculata* by searches of the literature, and searches of the herbaria of Auburn University (AUA), the University of Alabama (UNA), the University of Georgia (GA), Troy University (TROY), and the University of

South Florida (USF). In addition, reports were obtained from The Alabama Natural Heritage Program, The Georgia Natural Heritage Program, The Florida Natural Areas Inventory, and knowledgeable individuals. Furthermore, extensive surveys of areas near or between existing populations were conducted with particular emphasis on sites up- or down-stream. Counties adjoining those containing known populations were also extensively searched, including large areas of the Florida Panhandle south of the Covington and Geneva County, Alabama populations. Voucher specimens of all newly discovered populations were deposited at TROY or AUA, with duplicates to the Vanderbilt University Herbarium (VDB), the Jacksonville State University Herbarium (JSU), and UNA.

Average annual and monthly data from the National Weather Service at Auburn University were obtained for precipitation and temperature at sites near the extreme ends of the species' range in order to characterize the climate pattern. Precipitation averages were obtained for St. Clair and Covington Counties in Alabama, while temperature averages were obtained for Birmingham in Jefferson County, and Andalusia in Covington County, Alabama. These represent the nearest reporting stations from which data were available for the southern-most and northern-most populations.

Census of flowering individuals and population trends

Population estimates utilizing large reproductive individuals can provide a gross index of population trends, and are more uniform among observers than estimates of the total number of individuals (Elzinga *et al.*1999). Because *R. auriculata* reproduces asexually through the production of short rhizomes (Kral 1983), the determination of genetic individuals was impossible in the field. Previous research has reported that most populations consist of large clones and that most reproduction is asexual (Kral 1983, Schotz 2000). However, regardless if produced sexually or asexually, each rosette produces a single flowering stem each season. I chose to assess the size, health, and vigor of populations over time through the counting of flowering stems.

In addition, the number of flowering stems can provide information on the health and vigor of populations, since this species does not flower until at least two years old from seed and will not flower if growing in deep shade (based upon personal observations of plants in the field and under cultivation). Individuals produced asexually will flower in the summer following their production the previous autumn (A. Diamond, pers. obs.). Once plants begin to flower, they continue to flower yearly as long as conditions remain favorable (based upon personal observations of plants in the field and under cultivation). Populations were visited annually from 1998 to 2002 in early August, during peak flowering. A census of the number of inflorescences was obtained at each site by directly counting at smaller sites or by visual estimation at the largest sites. These data were compared with other data from previous years to determine population trends.

Associated vegetation

The community in which *R. auriculata* grows was described by sampling the associated vegetation using one by two meter quadrats at 20 sites (Table 1). Sample quadrats were centered on *R. auriculata* clumps with the long axis parallel to the adjacent water body. Estimated percent cover by each vascular plant species, and by bare soil or water, was recorded. At the largest sites, transects were arranged parallel to the long axis of the population and quadrats were located randomly to either the right or left sides of the transect at three meter intervals. Data on associated species were only collected from quadrats containing *R. auriculata* plants. A minimum of 25% of each population was sampled, based upon a visual estimation of the total area occupied by *R. auriculata* at each site. At sites with small populations, the entire area was sampled utilizing one by two meter quadrats centered over each clump or aggregate of clumps.

Sorensen's Index of Similarity (IS) was used to calculate floristic similarities among the populations (Mueller-Dombois and Ellenberg 1974). These values were used to generate a hierarchical cluster analysis dendrogram using average linkage between groups (SPSS for Windows, 11.0.1, Standard Version). Importance values (IV) based on relative cover and relative frequency were calculated for each species. The IV for each species was calculated in two ways: one based on sites (n = 20) and the other based on the total number of quadrats used (n = 88). In addition, non-native species were identified based upon information presented in Kartesz (1999) and the U. S. Department of Agriculture Natural Resources Conservation Service's PLANTS Database (U. S. Department of Agriculture 2002a). Nomenclature follows Kartesz (1994).

Soil analysis

Soil series associated with *R. auriculata* were determined by examining county soil maps where available. Soil samples were collected from the 20 sites selected for vegetation analysis and sent to the Soil Testing Lab at Auburn University for analysis of soil group, pH, and extractable phosphorus, potassium, magnesium, and calcium. At each site a minimum of three samples were taken spanning the area of the population. Each sample was collected within the root zone of a clump of *R. auriculata* plants. Soil was collected to a depth of 25-30 cm with a small shovel. Organic matter (if any) on the surface was removed prior to obtaining samples and any large roots, rocks, or woody debris were removed from the sample. The samples were mixed and a single sub-sample from each site was analyzed.

RESULTS

Distribution

The range of *R. auriculata* is disjunct with one center of populations occurring in southern Alabama and adjacent areas of Florida and Georgia, and the second center located in north-central Alabama. *Rudbeckia auriculata* occurs in upland physiographic provinces of Alabama as well as on the East Gulf Coastal Plain of Alabama, Florida, and Georgia. It can be found in a variety of open, sunny, wetland habitats including pitcher plant bogs, wet calcareous outcrops and the edges of hardwood flood plain forests (Table 1). However, it occurs most often in human-disturbed areas such as roadsides and power line corridors (Schotz 2000). Presently there are 32 known current or historical sites for *R. auriculata*. Thirty of these sites occur in Alabama, one in Georgia, and one in Florida (Fig. 1). A total of 12 counties in these three states have supported one or more populations of *R. auriculata* (Table 1). All but one of the previously reported sites was relocated during this study. The site not relocated had insufficient location information, being reported simply as “clear-cut to the south of Luverne” (McDaniel 1981).

The Alabama county distribution of *R. auriculata* includes the following physiographic provinces: Chunnenuggee Hills District of the East Gulf Coastal Plain (Barbour and Bullock Counties), Southern Red Hills District of the East Gulf Coastal Plain (Crenshaw and Pike Counties), Dougherty Plain District of the East Gulf Coastal Plain (Covington and Geneva Counties), Cahaba Valley District of the Alabama Valley and Ridge (Bibb, Jefferson, St. Clair, and Shelby Counties), and Sand Mountain District of the Cumberland Plateau (Blount County) (Cartographic Research Laboratory 1975). The Webster County, Georgia, site is located within the Fall Line Hills District of the East Gulf Coastal Plain (Clark and Zisa 1976). The Walton County, Florida, site is located in the Dougherty Karst District of the East Gulf Coastal Plain (Brooks 1981).

The climate throughout the range of *R. auriculata* is humid sub-tropical with long hot summers and short cool winters. The Gulf of Mexico serves to moderate the climate of the area. Precipitation is fairly constant throughout the year, with the wettest months being December through March and the driest month being October. Most precipitation falls in the form of rain. Near the northern limit of the species' range, in St. Clair County (AL), average annual precipitation is 132.5 cm compared to 149.8 cm in Covington County (AL), near the southern limit of the species' range. Average daily temperature in January for Birmingham, the nearest reporting station to the Leeds population, is 5.8 °C, and is 8.4°C for Andalusia, the nearest reporting station to the southern populations. Average daily July temperature for both Birmingham and Andalusia is 26.8° C.

Population trends

The first data on the size of populations of *R. auriculata* are in McDaniel's 1981 status report for the U.S. Fish and Wildlife Service (McDaniel 1981). Based on 1980 data, he estimated 2,652 flowering stems in five populations (Table 2). At the time of his report, 11 populations were known in Alabama (Table 1). Over ten years later (in 1992), I visited 14 of the then 16 known populations and estimated 1,363 flowering stems at those populations (Table 2).

By 1996 the number of known populations had increased to 22, including the first report from outside of Alabama (Table 1). In that year I visited 17 sites and obtained data on one additional population. The number of flowering stems at these populations was estimated at 3,297 (Table 2). In 1998 I visited 18 of the then 25 known populations and received data on two additional populations from their discoverers. The number of flowering stems at all known populations was estimated at 2,931 (Table 2). In 1999, 21 of 26 reported populations were visited, and I estimated 2,818 flowering stems at these populations.

In 2000, the second population outside of Alabama was reported (Table 1). That year I visited 25 of the 27 populations and received data for the Florida population from its discoverer. This is the first year that a complete census of all currently known and locatable populations occurred. An estimated 1,527 flowering stems were observed (Table 2). In 2001 the total number of known populations was 29 (Table 1), and I visited all of the locatable populations and recorded 1,756 flowering stems (Table 2). In 2002, the number of populations reached 32 (Table 1). All locatable sites were visited and 5,552 flowering stems were recorded. This was the largest number of flowering stems and populations recorded during this study (Table 2). However between the years of 1980 and 2002, while the number of known populations of *R. auriculata* had increased from 11 to 32, the total number of flowering stems averaged only 2,335.

Of the 32 known populations, six are believed to be extirpated. The population with two flowering stems reported by McDaniel (1981) from “south of Luverne” in Crenshaw County has never been relocated despite extensive yearly searches. Five populations whose exact location had been observed by me have also disappeared. The population at Sansom in Geneva County, Alabama, was last observed in 1992 when it produced three flowering stems. The population at Lugo in Barbour County, Alabama, was last observed in 1999, and the Pike County Lake population in Pike County, Alabama, was last observed in 2000, when each population produced a single flowering stem. The population on Gin Creek in Crenshaw County, Alabama has not been observed since its original discovery in 1996 when it produced three flowering stems. Likewise the population in Walton County, Florida has not been observed since its discovery in 2000 when it produced four flowering stems. While plants may remain vegetative for a number of years without producing flowering stems, annual searches of these sites since their last observation have revealed no basal rosettes. Other populations which have demonstrated a decline include the Alabama populations at Blountsville in Blount County, Red Level and Richland Creek in Covington County, Poplar Creek in Geneva County, and Alabama Hwy. 10 and Tick Hill in Pike County (Table 2).

A few of the populations, such as Rutledge and Patsaliga River in Crenshaw County, Alabama, and Sandy Run Creek in Pike County, Alabama have remained relatively stable since their discovery (Table 2). The Florala population in Covington County, Alabama, has increased (Table 2), possibly due to alteration of the habitat and removal of competing vegetation during the construction of a home and associated pond (A. Diamond pers. obs., Schotz 2000). However, the long-term future of this population is unsure, as development of the site continues. The Hwy. 107 and Dirt Road populations in Shelby County, Alabama, have increased, but no trend can be determined due to the low number of observations (Table 2). Populations often fluctuate greatly in the number of flowering stems from year to year due to disturbance, succession, and possibly other factors such as precipitation (Table 2).

Associated vegetation

Most species associated with *R. auriculata* are common wetland species that frequent open, sunny locations. Sampling of 20 of the known *R. auriculata* sites resulted in the documentation of 138 species of vascular plant associates (Table 3). According to the National List of Vascular Plant Species that Occur in Wetlands (U. S. Fish and Wildlife Service 1988), 37 (27%) are obligate wetland species which occur almost always under natural conditions in wetlands; 37 (27%) are facultative wetland species which usually occur in wetlands but are occasionally found in non-wetlands; 42 (30%) are facultative species which are equally likely to occur in wetlands or non-wetlands; and 10 (7%) are facultative upland species that usually occur in non-wetlands but are occasionally found in wetlands. Twelve taxa identified during the surveys were not on the wetlands plant list, but of this number three were not determined to species and one was not determined to genus.

A diverse assemblage of mainly wetland plant species resulted from sampling. Sixty-four (46%) of the 138 species collected were found at only one site and another 58 (42%) were found at between two and five sites. Thirteen species (9%) were found between at six and nine sites. Only three species (2%) were found at 10 or more of the 20 sites. These were *Alnus serrulata* (Ait.) Willd., *Juncus effusus* L., and *Rubus argutus* Link. All three species are widespread in eastern North America (Kartesz 1999) and thus would not serve as indicator species for *R. auriculata.* The 10 species with the highest average percent cover for all sites combined were *Alnus serrulata* (11.9%), *R. auriculata* (9.8%), *Acer negundo* L. (5.9%), *Salix nigra* Marsh. (4.8%), *Juncus effusus* (4.4%), *Clematis virginiana* L. (3.7%), *Leersia oryzoides* (L.) Sw. (3.8%), *Ligustrum sinense*

Lour. (3.5%), *Panicum microcarpon* Muhl. ex Ell. (2.5%), and *Rubus argutus* (2.5%). Together they accounted for 52.8% of mean total percent cover. All of these species are classified as shade intolerant (U. S. Department of Agriculture, Natural Resources Conservation Service 2002a), except for *Acer negundo* which is reported as shade tolerant, *Clematis virginiana* which is reported as intermediate, and *Ligustrum sinense* and *R. auriculata* for which no shade tolerance was reported. These species are also common wetland species and thus would not be good indicators for *R. auriculata* (Godfrey and Wooten 1981, 1979). This diversity of associated species is likely the result of the number of physiographic provinces that *R. auriculata* occupies, the different stages of succession found at each site, and the variety of soil types on which the populations occur.

The species with the 10 highest IVs for sites and quadrats were *Acer negundo*, *Alnus serrulata*, *Clematis virginiana*, *Juncus effusus*, *Juncus validus* Coville, *Leersia oryzoides*, *Ligustrum sinense*, *Rubus argutus*, *Salix nigra* and *Solidago canadensis* L. The index of similarity and dendrogram (Fig. 2) generally revealed that sites in closest geographic proximity to each other were most similar. The northern Alabama sites formed one cluster and the southern Alabama and Georgia sites formed another. This is as expected due to the similar soils and vegetation in each region. The only exceptions to this are the two Shelby County sites, which cluster with the southern Alabama and Georgia sites (Fig. 2). No readily apparent reason seems to exist for their unusual location in the dendrogram, grouping with geographically more distantly located sites.

Non-native species accounted for 7.2% of the total associates (10 species). This figure is lower than the 15 to 20 percent generally reported in county-level floras in

Alabama (Diamond 2003, Martin *et al.* 2002, Diamond and Freeman 1993). Non-native species associated with *R. auriculata* were *Albizia julibrissin* Durz., *Broussonetia papyrifera* (L.) L'Her. ex Vent., *Ligustrum sinense* Lour., *Lonicera japonica* Thunb., *Microstegium vimineum* (Trin.) A. Camus, *Myriophyllum aquaticum* (Vell.) Verdc., *Paspalum notatum* Fluegge, *Paspalum urvillei* Steud., *Phyllanthus urinaria* L. and *Verbena brasiliensis* Vell. All 10 of these non-native species are listed on the U. S. Department of Agriculture Natural Resources Conservation Service's PLANTS database Invasive Plants List (U. S. Department of Agriculture 2001).

Soil analysis

Soil surveys for five Alabama counties containing populations of *R. auriculata* were available. This information is summarized in Table 4. The soils vary considerably, but share the fact that all are hydric and often subject to flooding. Tanyard Silt Loam differs in that it is well-drained.

Soil samples collected and sent to the Auburn University Soil Testing Lab revealed great variation in texture, pH, and nutrient concentration (Table 5). At eight sites the soil texture was loam or light clay. Five of the sites were sandy soils and five were clays or soils high in organic matter. Two of the samples were heavy clays of the Black Belt. Thus, soil texture does not appear to be a significant limiting factor in the distribution of *R. auriculata*. Likewise, pH varied from a low of 4.6 at Bread Tray Hill in Bullock County to a high of 8.0 at Leeds in Jefferson County. Fourteen of the tested sites had soils that were slightly to strongly acidic and six were basic. Based upon these data, pH does not appear to be a limiting factor in the distribution of this species. Extractable nutrient concentration also varied considerably between the sites and no trend or pattern was discernible (Table 5).

DISCUSSION

Among the 50 states Alabama is ranked fifth in biodiversity, fourth in number of species at risk and second in total number of extinctions (Stein 2002). With respect to vascular plants, Stein (2002) estimated that 9.4% of the species in Alabama are at risk of extinction with the leading threats being habitat degradation and destruction, and the spread of invasive species. The range of *R. auriculata* is disjunct with one center of populations occurring in southern Alabama and adjacent areas of Florida and Georgia, and the second center located in north-central Alabama. This disjuncture appears to be genuine and not an artifact of collecting. Extensive surveys over a 10 year period resulted in the discovery of fourteen new populations, most located within a few kilometers of previously known sites. Due to its large stature and ease of visibility when in flower, the discovery of substantial numbers of new populations is unlikely.

Based upon soil data and associated species, one would expect *R. auriculata* to be more common than surveys indicate. It is not restricted to any one soil type, and occurs on soils with pH values ranging from acidic (4.6) to basic (8.0) (Table 5). The plant associates are common, widespread wetland species in the southeastern United States, and none were determined to be indicator species. However, of the 32 known populations surveyed in 2002, only 10 contained at least 100 flowering stems. Small populations are especially vulnerable to extinctions caused by local events and to reduction of genetic viability through inbreeding (Oostermeijer *et al.* 1998). Even in large populations, *R. auriculata* has a relatively low IV and is a minor community component (Table 3).

McDaniel (1981), in his report to the Fish and Wildlife Service, stated that *R. auriculata* can be so abundant as to occur in almost pure stands essentially without any significant associates, but that was not found to be the case in this study. Plot sampling of associated vegetation documented an IV for *R. auriculata* of only 27.3% for quadrats and 15.7% for sites, even though data were collected only from quadrats containing *R. auriculata*.

Why then is *R. auriculata* uncommon? *Rudbeckia auriculata* is not weedy in nature and seems to spread mostly by vegetative means (Schotz 2000). It does not seem to spread rapidly by way of seeds as newly-created openings produced by right-of-way maintenance and logging within and adjacent to populations of *R. auriculata* remained uncolonized (Diamond pers. obs., Schotz 2000). Thus achene viability and dispersal may be limiting factors. Natural successional toward hardwood forest also poses a threat to this species, and lack of natural disturbance may be a critical limiting factor. Field observations and reports of other researchers indicate that *R. auriculata* requires some form of disturbance and favors open sunny sites such as roadsides and power line right-of-ways (Schotz 2000, McDaniel 1981). *Rudbeckia auriculata* does not flower and does not persist for long periods when the canopy closes (A. Diamond pers. obs., Schotz 2000). Kral stated that the species "would not survive under the closed canopy of pine plantations" (Kral 1983). Most of the sites now supporting populations would become unsuitable for the continued existence of *R. auriculata* without some form of regular natural or human-caused disturbance.

There are other examples of rare sun-loving taxa associated with open roadside habitats in the southeastern United States (Jones 1994, DeSelm 1989). Campbell *et al.* (1991) discussed two hypotheses to explain rare taxa being found mostly on roadsides:

(1) that the plants invaded the disturbed areas after European settlement, and/or (2) that the plants are relicts from natural openings maintained by fires. One of the least human-impacted *R. auriculata* sites was Sarracenia in Geneva County, Alabama. This population occurred in a pitcher plant (*Sarracenia leucophylla* Raf.) bog, a habitat maintained in an open sunny state by periodic fire during summer droughts. However, most of the other sites occupied by *R. auriculata* are too wet to burn frequently, occurring on low floodplains and in swampy areas.

Along with windstorms and fire, beavers (*Castor canadensis* Kuhl) are major natural agents responsible for disturbance in eastern North America (Kiviat 1978, Kaye 1962). Ten of the 32 populations of *R. auriculata* are located near active or abandoned beaver ponds and are subjected to periodic disturbance through the animals' activity (A. Diamond, pers. obs.). Beavers have been shown to increase landscape heterogeneity (Remillard *et al.*1987) and perhaps they play a key role in providing early successional habitat essential for *R. auriculata*. Wright *et al.* (2002) determined that beaver activity increased the number of herbaceous species in the riparian zone by over 33%. The importance of beaver-created habitat has been well documented (Johnson and Naiman 1990, Barnes and Dibble 1988, Whitaker 1988, Wilkinson 1962, Gard 1961). However, in Alabama beavers had been extensively trapped by the late 1800's and were extremely scarce. In 1938 the Alabama Department of Conservation estimated that fewer than 500 beavers remained in the entire state (Sievering 1989). Perhaps the current distribution of *R. auriculata* reflects the near disappearance of beavers and the early successional habitat they created. Other forms of natural disturbance may be important at some sites. The calcareous outcrop area in Leeds, St. Clair County, Alabama, is a site with soils too thin to support woody arborescent vegetation and is subjected to frequent scouring from a nearby stream, keeping it in an open sunny condition.

Rudbeckia auriculata is also subject to a variety of other threats including the loss or degradation of its wetland habitat, the use of herbicides along roadsides and power line right-of-ways, and competition from invasive species (Schotz 2000). Half of Alabama's wetlands have been lost since 1780 (New Mexico Center for Wildlife Law 2003). Kral states that the species “would not survive site preparation involving drainage” (Kral 1983). Wetland loss can take the form of draining and conversion for cultivation or housing. The latter occurred to a portion of the Florala site in Covington County, where a home and associated pond were constructed on approximately 10% of the site. Development can also take the form of alteration for recreational use, as happened at the Pike County Lake site, where the population was apparently eliminated through repeated short mowing of the bank areas to improve access for fishing. The widening of highways, and the channeling of streams for storm water runoff, pose threats to some of the populations, especially those in or near urban areas that are experiencing rapid population growth (Schotz 2000).

A serious threat to the continued existence of *R. auriculata* is the use of herbicides to maintain roadside and power line right-of-ways, and to prepare sites for loblolly pine plantations. No populations were found on roadside or power line corridors that had been sprayed with herbicide, even though they appeared to be suitable habitat in all other aspects. The sharp limit of populations along roadside and power line corridors at the edge of the range of the sprayers is evidence that the populations were once larger and that some individuals had been eliminated due to herbicide use. Schotz (2000) stated that the disappearance of the Samson site may be due to "advanced forest succession and herbicide application by the state highway department." Infrequent bush-hogging of these areas seems to have no negative effect on the plants if conducted early enough in the year so as not to interfere with flowering. In fact, some disturbance that prevents the encroachment of woody vegetation seems necessary for the survival of this species (A. Diamond pers. obs., Schotz 2000). Appropriate management of roadside and power line right-of-way populations may become significant to the survival of the species.

Another potential threat to *R. auriculata* occurs in the form of invasive exotic plant species. Ten species listed on the U. S. Department of Agriculture's Natural Resources Conservation Service National Plant Data Centers Invasive Plants List (U. S. Department of Agriculture 2002a) have become established in certain populations. Of this number, privet (*Ligustrum sinense*) and Japanese stilt grass (*Microstegium vimineum* (Trin.) A. Camus) pose particular threats to *R. auriculata.* Privet forms dense stands in disturbed and natural wetlands in the southeastern United States (U. S. Department of Agriculture 2002b, Dirr 1983). The deep shade produced by the semi-evergreen privet may not only prevent establishment of *R. auriculata* seedlings, but also can suppress the flowering of established plants and may lead to their deaths (A. Diamond pers. obs.). Japanese stilt grass forms dense mats in moist areas that can prevent the establishment of native species (Tu 2000). Both of these species are difficult to eradicate from wetlands after they have become established (U. S. Department of Agriculture 2002b, Tu 2000).

Herbivores can significantly influence the abundance of plants, including species that are rare (Bevill *et al.* 1999). Damage due to native herbivores was not observed to be a major problem in natural populations of *R. auriculata* during this study (A. Diamond, pers. obs., Schotz 2000). However, cultivated plants suffered extensive defoliation due to whitetail deer (*Odocoileus virginianus* Boddaert). Studies have indicated that whitetail deer herbivory may be more severe for small plant populations than for large ones (Fletcher *et al.* 2001, Loeffler and Brett 2000). This may become of greater concern in the future when captive propagation and re-introductions may become necessary for the continued existence of this species. The Alabama Department of Conservation and Natural Resources estimates deer densities in excess of 30 animals per 2.59 km^2 in the southern portion of the state (Alabama DCNR 2000). A single whitetail deer can consume between 3.75 and 5.44 kg of plant material daily and Alabama's estimated 2.8 million whitetail deer can therefore consume over 3810 kilotonnes of food annually, most of which is native plant material (Thomas 2003).

In Crenshaw County, Alabama, where a power line right-of-way crossed a grazed pasture, *R. auriculata* was absent from the pasture yet was abundant outside the fence in all directions. The presence of other tall perennial herbs in the pasture that are not readily consumed by these animals, such as *Eupatorium* and *Rubus,* indicated that grazing was responsible for the absence of *R. auriculata* and not other factors such as mowing. Other sites that are located in abandoned or little-used pastures include Sandy Run Creek in Pike County, Alabama, and Hwy. 107, Hwy. 22, and Dirt Road in Shelby County, Alabama. The possible return of these areas to heavy grazing may threaten these populations in the future and they should be monitored.

Most populations of *R. auriculata* are small and occur on unprotected and disturbed sites such as highway right-of-ways and power line corridors. Of the 19 populations visited by Schotz between 1998 and 2000, only two were considered as “excellent” and two as “good” based upon the Nature Conservancy’s element occurrence ranking system (Schotz 2000). Most populations remain vulnerable to destruction from human activities. Only three of the 32 known populations occur on public property or protected areas. The Cahaba/Blackwater Land Trust has purchased the Turkey Creek site in Jefferson County, and the Ebenezer Church site in Shelby County is now a part of an ecological preserve managed by the University of Montevallo. The continued existence of these two populations seems secure at this time. However, even when publicly owned, populations may be vulnerable. The Pike County Lake population, now believed to be extirpated due to repeated short mowing, occurred on a public fishing lake owned by the Alabama Department of Conservation and Natural Resources.

The Endangered Species Act of 1973 states that endangered or threatened status is based upon the following factors: (1) the present or threatened destruction, modification, or curtailment of a species’ habitat or range; (2) overutilization of a species for commercial, recreational, scientific, or educational purposes; (3) disease or predation that causes the decline of a species; (4) the inadequacy of existing regulatory mechanisms to protect a species; and (5) other natural or manmade factors affecting a species’ continued existence (U. S. Fish and Wildlife Service 2003a). My findings document the lack of increase in most individual population sizes over time, along with the loss of some populations and the modification of the habitat of others. In Alabama, where the majority of the populations of *R. auriculata* occur, no state conservation laws or legislation exist for the protection of native plant species. Alabama does not have an endangered species act, and there are no penalties for taking species listed by the Natural Heritage Program as rare, threatened or endangered (New Mexico Center for Wildlife Law 2003). This lack of existing regulatory mechanisms, coupled with threats from human activities and introduced species and the fact that most populations are small and occur on marginal habitat, causes me to agree with Schotz (2000) that the U. S. Fish and Wildlife Service should re-evaluate *R. auriculata* and consider providing it some form of formal protection.

Figure 1: Distribution by county of *Rudbeckia auriculata* (Perdue) Kral in the southeastern United States.

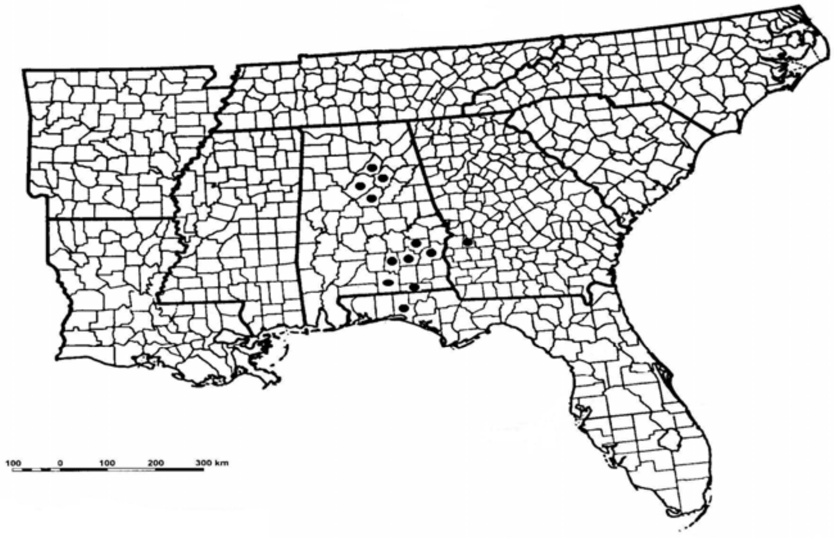

Figure 2: Dendrogram of vegetation similarity of *R. auriculata* populations using Average Linkage (Between Groups). Sorensen's index of similarity (IS) was used to calculate floristic similarities among the populations and these values were used to generate a hierarchical cluster analysis (SPSS for Windows, 11.0.1, Standard Version).

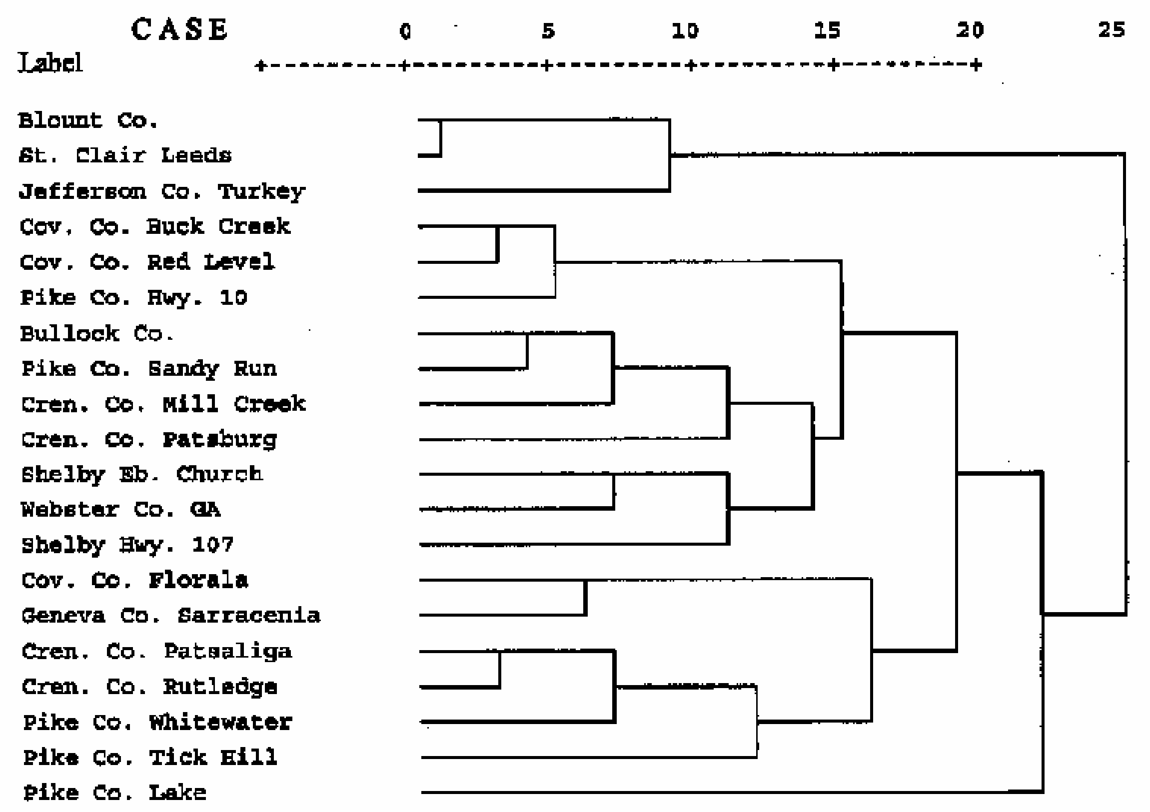

Table 1: Distribution data for *Rudbeckia auriculata*. Sites are listed alphabetically by county, then by site name. Date of discovery, name of discoverer, first known herbarium specimen or publication reference, and habitat description are also presented. Sample sites for associated vegetation and soils are indicated with an asterisk following the site name.

County	**Site Name**	**Date of Discovery/ Discoverer**	**Specimen or Publication**	**Habitat Description**
Barbour Co. Alabama	Lugo	12 Sept. 1968/ Kral and Blum	Kral and Blum 33300 (VDB)	Roadside ditch.
Blount Co. Alabama	Blountsville *	15 Aug. 1998/ Keener	Keener 1472 (UNA)	Roadside edge of a wetland. Old beaver pond?
Bullock Co. Alabama	Bread Tray Hill*	17 Aug. 1993/ Diamond	Diamond 8742 (AUA)	Around and below a man-made pond.
Covington Co. Alabama	Red Level*	24 July 1958/ Perdue	Perdue 2177 (FSU, US)	Roadside near a small stream.
	Buck Creek*	14 Aug. 1999/ Diamond	Diamond 11879 (TROY)	Roadside edge of an old beaver pond.
	Florala	24 July 1968/ Kral	Kral 31970 (VDB)	Roadside and disturbed area near a small stream
	Richland Creek	25 June 1964/ Godfrey and Clewell	Godfrey and Clewell 64392 (USF)	Roadside along a small stream.
Crenshaw Co. Alabama	Rutledge*	8 Aug. 1992/ Diamond and Freeman	Diamond 8380 (AUA)	Power line right-of-way near a beaver pond.
	Patsaliga River*	16 Aug. 1968/ Kral	Kral 32421 (VDB)	Roadside near a beaver pond.
	Mill Creek*	9 Aug. 1980/ McDaniel and Haynes	McDaniel and Haynes 24311 (IBE)	Roadside along a small stream.
	Patsburg*	17 Aug. 1992/ Diamond	Diamond 8400 (AUA)	Roadside below a man made pond.
	Gin Creek	25 Aug. 1996/ Diamond	Diamond 10501 (AUA)	Roadside near a small stream.
	S. Luverne	1980/ McDaniel	McDaniel 1981	Clear cut.

Geneva Co. Alabama	Sansom	3 Sept. 1966/ Kral	Kral 36837 (FSU, VDB)	Roadside near a small stream.
	Poplar Creek	7 Aug. 1998/ Schotz	Schotz 2000	Power line right-of-way near a small stream.
	Sarracenia*	12 Aug. 1966/ McDaniel	McDaniel 7657 (IBE)	Along a small stream in a pitcher plant bog converted to a pine plantation. Now present only at roadside.
Jefferson Co. Alabama	Leeds 1	7 Aug. 2001/ Diamond	Diamond 12597 (TROY)	Disturbed areas along a small creek.
	Leeds 2	11 Aug. 2002/ Diamond	Diamond 13536 (TROY)	Disturbed areas along a small creek.
	Sweeny Hollow	11 Aug. 2002/ Diamond	Diamond 13533 (TROY)	Roadside along a small creek.
	Turkey Creek*	24 Oct. 1996/ Oberholster	Diamond 12604 (TROY)	Around a spring complex and beaver pond on a small stream.
Pike Co. Alabama	White Water Creek*	9 Aug. 1992/ Diamond	Diamond 8387 (AUA)	Roadside along a small creek.
	Pike County Lake*	10 Sept. 1968/ Kral	Kral 33174 (VDB)	Bank of a man-made impoundment.
	Sandy Run Creek*	23 Aug. 1989/ Diamond	Diamond 6297 (AUA)	Roadside, power line right-of-way and disturbed area in a pasture along a small creek and old beaver pond.
	Ala. Hwy. 10*	11 Aug. 1996/ Diamond	Diamond 10443 (AUA)	Roadside at the edge of a beaver pond.
	Tick Hill*	12 Sept. 1990/ Diamond	Diamond 7124 (AUA)	Edge of an old beaver pond.
St. Clair Co. Alabama	Leeds*	27 Sept. 1972/ Kral	Kral 48579 (VDB)	Shallow soil over calcareous outcrop along a small creek.
Shelby Co. Alabama	Ebenezer Church*	5 Oct. 1993/ Allison	Diamond 11986 (TROY)	Edge of a beaver pond.
	Hwy. 107*	29 July 1997/ Oberholster	Diamond 12599 (TROY)	Along a small creek in a pasture and edge of a beaver pond.
	Hwy. 22	7 Aug. 2001/ Diamond	Diamond 12600 (TROY)	Along a small creek in a pasture.
	Dirt road	7 Aug. 2001/ Diamond	Diamond 12601 (TROY)	Along a small creek in a pasture.
Walton Co. Florida	U.S. 331	17 Aug. 2000/ Searcy	Searcy (USF)	Roadside along a small creek.
Webster Co. Georgia	Plains*	9 Sept. 1996/ Allison	Allison 9473 (UGA)	Roadside along a small creek.

Table 2: Numbers of flowering stems for populations of *Rudbeckia auriculata*. Data for 1980 are from McDaniel (1981). Data in bold are from Nature Conservancy personnel. Data from Blountsville for 1998 and U. S. 331 for 2000 are from the discoverer of those populations. All other counts are by the author.

County and Site	Year								
	1980	1992	1996	1997	1998	1999	2000	2001	2002
Barbour Co. Alabama									
Lugo		7	0		0	1	0	0	0
Blount Co. Alabama									
Blountsville					12		0	0	0
Bullock Co. Alabama									
Bread Tray Hill			75		7	0	25	34	87
Covington Co. Alabama									
Red Level		10	10		3	10	0	0	0
Buck Creek						2	5	0	12
Florala		7	500		150	1000	20	75	1000
Richland Creek		10	75		28	7	0	0	0
Crenshaw Co. Alabama									
Rutledge		1000	1000		1000	1000	1000	1000	500
Patsaliga River	50	50	50		37	100	225	150	150
Mill Creek	500	0	10		32	45	75	50	75

Patsburg		20	12		16	35	14	10	42
Gin Creek			3		0	0	0	0	0
S. Luverne	2								
Geneva Co. Alabama									
Sansom		3	0		0	0	0	0	0
Poplar Creek					**600**	0	0	0	0
Sarracenia		20	18		17	10	60	7	12
Jefferson Co. Alabama									
Leeds 1								7	29
Leeds 2									1000
Sweeny Hollow									500
Turkey Creek			500				7	37	0
Pike Co. Alabama									
White Water Creek		12	25		19	45	35	37	2
Pike County Lake	100	20	0		0	0	1	0	0
Sandy Run Creek		200	1000		1000	500	8	250	1000
Ala. Hwy. 10					3	10	0	0	7
Tick Hill		4	11		7	5	9	0	0
St. Clair Co. Alabama									
Leeds	1000					24	6	7	11
Shelby Co. Alabama									

Ebenezer Church				**500**			9	23	250
Hwy. 107							6	21	500
Hwy. 22								3	0
Dirt Road								35	250
Walton Co. Florida									
U.S. 331							4	0	0
Webster Co. Georgia									
Plains			**8**				12	10	125
Total number of flowering stems	2652	1363	3297	500	2931	2818	1527	1756	5552

Table 3: Importance Values (IV) of vascular plant species associated with *Rudbeckia auriculata* and their wetland indicator status. Non-native species are indicated by an asterisk to the left of the entry. Wetland indicator status of associated species was determined utilizing the National List of Vascular Plant Species that Occur in Wetlands (U. S. Fish and Wildlife Service 1988). Status codes are:

Obligate Wetland (OBL). Occur almost always (estimated probability >99%) under natural conditions in wetlands; Facultative Wetland (FACW). Usually occur in wetlands (estimated probability 67%-99%), but occasionally found in non-wetlands; Facultative (FAC). Equally likely to occur in wetlands or non-wetlands (estimated probability 34%-66%); and Facultative Upland (FACU). Usually occur in non-wetlands (estimated probability 67%-99%), but occasionally found in wetlands (estimated probability 1%-33%).

Scientific Name	Number of sites present (out of 20)	Wetland indicator status	IV for quadrats as % (N = 88)	IV for sites as % (N = 20)
Acer negundo L.	3	FACW	3.68	6.99
Acer rubrum L.	6	FAC	3.69	2.51
Agalinis fasciculata (Ell.) Raf.	1	FACU	0.18	0.40
* *Albizia julibrissin* Durz.	2	None	0.32	0.63
Alnus serrulata (Ait.) Willd.	13	FACW	11.64	16.04
Ambrosia artemisiifolia L.	3	FACU	0.71	1.04
Ambrosia trifida L.	1	FAC	0.44	0.72
Ampelopsis arborea (L.) Koehne	6	FAC	2.68	2.58
Andropogon glomeratus (Walt.) B.S.P.	6	FACW	1.14	2.31
Apios americana Medik.	9	FACW	3.66	3.22
Arundinaria gigantea (Walt.) Muhl.	1	FACW	0.14	0.38
Aster lateriflorus (L.) Britt.	7	FAC	3.27	3.01
Axonopus fissifolius (Raddi) Kuhlm.	3	FACW	0.61	1.05
Baccharis halimifolia L.	2	FAC	0.28	0.55
Berchemia scandens (Hill) K. Koch	2	FACW	0.28	0.55
Betula nigra L.	2	FACW	1.30	1.43
Boehmeria cylindrica (L.) Sw.	5	FACW	1.94	2.11
* *Broussonetia papyrifera* (L.) L'Hér. ex Vent.	1	None	0.60	0.97

Callicarpa americana L.	1	FACU	0.18	0.34
Campsis radicans (L.) Seem. ex Bureau	4	FAC	1.10	1.42
Carex glaucescens Ell.	2	OBL	0.45	0.64
Carex lurida Wahlenb.	4	OBL	3.38	1.71
Carpinus caroliniana Walt.	2	FAC	0.28	0.55
Cephalanthus occidentalis L.	5	OBL	1.18	1.81
Chamaesyce hyssopifolia (L.) Small	1	None	0.20	0.39
Ciclospermum leptophyllum (Pers.) Sprague ex Britt. & Wilson	1	FAC	1.88	0.54
Cicuta maculata L.	2	OBL	0.82	0.69
Clematis crispa L.	1	FACW	0.15	0.58
Clematis virginiana L.	6	FAC	5.41	5.19
Conyza canadensis (L.) Cronq.	2	FACU	0.81	0.77
Cornus amomum P. Mill.	2	FACW	0.84	3.00
Cornus foemina P. Mill.	6	FACW	2.39	2.99
Cuscuta compacta Juss. ex Choisy	1	None	0.14	0.38
Cyperus haspan L.	1	OBL	0.31	0.29
Cyperus strigosus L.	1	FACW	0.13	0.27
Desmodium laevigatum (Nutt.) DC.	1	None	0.14	0.30
Dichanthelium dichotomum (L.) Gould	1	FAC	0.72	2.90
D. scoparium (Lam.) Gould	7	FACW	4.28	2.95
Digitaria ciliaris (Retz.) Koel.	1	FAC	0.18	0.34
Diodia virginiana L.	3	FACW	1.54	1.56
Diospyros virginiana L.	2	FAC	0.56	0.81
Eleocharis obtusa (Willd.) J.A. Schultes	1	OBL	0.56	0.45
Erechtites hieraciifolia (L.) Raf. ex DC.	2	FAC	0.25	0.56
Eriocaulon compressum Lam.	1	OBL	0.14	0.29
Eryngium yuccifolium Michx.	1	FAC	0.13	0.28
Eupatorium capillifolium (Lam.) Small	3	FACU	1.27	1.20
Eupatorium coelestinum L.	3	FAC	1.24	0.87
Eupatorium compositifolium Walt.	2	FAC	0.26	0.60
Eupatorium fistulosum Barratt	1	FAC	0.18	0.34
Eupatorium perfoliatum L.	1	FACW	0.24	0.40
Eupatorium serotinum Michx.	1	FAC	0.13	0.28
Euthamia tenuifolia (Pursh) Nutt.	1	FACW	0.15	0.30
Galium tinctorium (L.) Scop.	1	FACW	0.43	0.29
Helenium autumnale L.	4	FACW	2.36	1.82
Helianthus angustifolius L.	2	FAC	0.56	0.66
Hydrocotyle verticillata Thunb.	2	OBL	1.23	0.94
Hydrolea quadrivalvis Walt.	1	OBL	1.67	0.31
Hypericum mutilum L.	4	FACW	2.01	1.73
Hyptis alata (Raf.) Shinners	3	OBL	2.01	1.24
Impatiens capensis Meerb.	5	FACW	2.66	2.74
Ipomoea hederacea Jacq.	1	FAC	0.13	0.27
Iris hexagona Walt.	1	OBL	0.18	0.36
Itea virginica L.	2	FACW	0.96	1.99
Juncus acuminatus Michx.	2	OBL	1.21	0.40
Juncus sp.	1	None	0.86	0.37
Juncus effusus L.	10	FACW	10.44	7.30
Juncus elliottii Chapman	3	OBL	0.68	0.92
Juncus validus Coville	1	FACW	6.62	0.41
Justicia ovata (Walt.) Lindau	1	OBL	0.13	0.29

Lactuca canadensis L.	1	FACU	0.13	0.29
Leersia oryzoides (L.) Sw.	6	OBL	5.57	5.68
* *Ligustrum sinense* Lour.	5	FAC	3.26	5.08
Linum medium (Planch.) Britt.	1	FAC	0.39	0.28
Liquidambar styraciflua L.	4	FAC	1.37	2.01
Liriodendron tulipifera L.	2	FAC	0.49	0.66
* *Lonicera japonica* Thunb.	8	FAC	3.44	3.72
Ludwigia alternifolia L.	3	OBL	0.83	1.07
Ludwigia glandulosa Walt.	2	OBL	1.29	0.60
Ludwigia microcarpa Michx.	1	OBL	0.40	0.28
Ludwigia pilosa Walt.	1	OBL	0.18	0.32
Micranthemum umbrosum (J. F. Gmel.) Blake	1	OBL	0.18	0.29
* *Microstegium vimineum* (Trin.) A. Camus	1	None	0.14	0.32
Mikania scandens (L.) Willd.	8	FACW	3.15	3.94
Mitreola petiolata (J. F. Gmel.) Torr. & Gray	2	FACW	0.64	0.62
Myrica cerifera L.	1	FAC	1.93	2.55
* *Myriophyllum aquaticum* (Vell.) Verdc.	1	OBL	0.41	0.52
Nyssa sylvatica Marsh.	2	FAC	0.31	0.65
Onoclea sensibilis L.	3	FACW	0.64	0.93
Orontium aquaticum L.	1	OBL	0.15	0.32
Osmunda regalis L.	1	OBL	0.13	0.32
Panicum virgatum L.	1	FAC	0.54	0.53
Parthenocissus quinquefolia (L.) Planch.	1	FAC	0.18	0.32
* *Paspalum notatum* Flueggé	3	FACU	1.02	2.31
* *Paspalum urvillei* Steud.	5	FAC	3.90	3.03
Peltandra virginica (L.) Schott.	3	OBL	0.81	1.13
* *Phyllanthus urinaria* L.	1	FAC	0.18	0.36
Pinus sp.	1	None	0.25	0.27
Pinus taeda L.	1	FAC	0.60	0.97
Platanus occidentalis L.	2	FACW	0.42	0.86
Polygonum sp.	1	None	0.41	0.29
Polygonum setaceum Baldw.	1	FACW	0.26	0.28
Pteridium aquilinum (L.) Kuhn	1	FACU	0.30	0.47
Rhexia mariana L.	3	FACW	0.39	0.88
Rhexia virginica L.	2	FACW	0.26	0.60
Rhynchospora corniculata (Lam.) Gray	2	OBL	0.94	1.34
Rhynchospora glomerata (L.) Vahl	2	OBL	2.52	1.34
Rosa palustris Marsh.	2	OBL	0.76	0.62
Rubus argutus Link	11	FAC	1.50	1.22
Rubus cuneifolius Pursh	1	FACU	4.81	5.63
Rubus trivialis Michx.	1	FAC	0.15	0.28
Rudbeckia auriculata (Perdue) Kral	20	FACW	27.33	15.68
Ruellia caroliniensis (J. F. Gmel.) Steud.	1	None	0.13	0.28
Sabatia calycina (Lam.) Heller	1	OBL	0.27	0.28
Saccharum giganteum (Walt.) Pers.	2	FACW	0.70	0.83
Sagittaria latifolia Willd.	3	OBL	0.98	0.64
Salix eriocephala Michx.	2	FACW	0.15	0.28
Salix nigra Marsh.	8	OBL	6.72	7.24
Salvia lyrata L.	1	FAC	0.26	0.29
Sambucus canadensis L.	4	FACW	0.93	1.11
Saururus cernuus L.	2	OBL	0.41	0.59
Scirpus cyperinus (L.) Kunth	3	OBL	1.42	1.02

Selaginella apoda (L.) Spring.	1	FACW	0.15	0.28
Setaria parviflora (Poir.) Kerguélen	1	FAC	0.63	0.57
Solidago canadensis L.	8	FACU	6.72	7.24
Solidago rugosa P. Mill.	2	FAC	2.42	1.47
Taxodium distichum (L.) Rich.	1	OBL	0.15	0.28
Toxicodendron radicans (L.) Kuntze	4	FAC	0.94	1.34
Triadenum walteri (J. G. Gmel.) Gleason	1	OBL	0.24	0.39
Typha latifolia L.	2	OBL	0.26	0.28
Ulmus americana L.	1	FACW	0.55	0.72
Unknown Poaceae	1	None	0.13	0.28
* *Verbena brasiliensis* Vell.	3	FAC	1.04	0.90
Verbena urticifolia L.	1	FAC	0.89	0.34
Vitis cinerea (Engelm.) Millard	1	FAC	0.18	0.40
Vitis rotundifolia Michx.	1	FAC	0.12	0.27
Wahlenbergia marginata (Thunb.) A. DC.	1	None	0.12	0.27
Wisteria frutescens (L.) Poir.	1	FACW	0.14	0.29
Woodwardia areolata (L.) T. Moore	1	OBL	0.42	1.59
Woodwardia virginica (L.) Smith	1	OBL	0.13	0.28

Table 4: Soil data from county soil surveys for Alabama sites currently supporting *Rudbeckia auriculata* populations.

County/ site	Soil type	pH	General comments
Covington/ Red Level Richland Creek	Muckalee Series	Strongly to very strongly acidic	Poorly drained soils subject to frequent flooding of brief duration (USDA 1989)
Covington/ Florala	Dorovan Muck	Strongly to very strongly acidic	Poorly drained organic soils subject to frequent flooding for extended periods of time (USDA 1989)
Pike/ all sites	Iuka-Kinston Complex	Acidic to strongly acidic	Deep poorly drained soils subject to frequent flooding (USDA 1992)
Geneva/ all sites	Ardilla Sandy Loam	Acidic	Deep poorly drained soils (USDA 1977)
St. Clair/ all sites	Tanyard Silt Loam	Neutral to strongly acidic	Deep well drained soils of flood plains (USDA 1985)
Shelby/ all sites	Tupelo Loam	Medium acidic to moderately alkaline	Deep poorly drained soils along drainage ways in areas underlain by limestone (USDA 1984)

Table 5: Soil data from twenty sites currently supporting *Rudbeckia auriculata* populations. Values for phosphorus, potassium, magnesium, and calcium are expressed as extractable nutrients (kilograms per hectare).

County	Location/ Physiographic Province	Soil Group *	pH	P	K	Mg	Ca
Covington Co. Alabama	Buck Creek/Dougherty Plain district of the East Gulf Coastal Plain	1	5.8	1.1	7.9	16.8	112.1
	Florala/Dougherty Plain district of the East Gulf Coastal Plain	1	6.5	9.0	38.1	42.6	504.4
	Red Level/Dougherty Plain district of the East Gulf Coastal Plain	2	6.1	3.4	60.5	344.1	1378.6
Geneva Co. Alabama	Sarracenia/Dougherty Plain district of the East Gulf Coastal Plain	1	5.5	5.6	24.7	49.3	762.2
Crenshaw Co. Alabama	Mill Creek/ Southern Red Hills district of the East Gulf Coastal Plain	2	6.5	7.9	40.4	144.6	1625.2
	Patsaliga River/ Southern Red Hills district of the East Gulf Coastal Plain	1	6.2	3.4	11.2	19.1	795.8
	Patsburg/ Southern Red Hills district of the East Gulf Coastal Plain	2	7.3	1.1	14.6	178.2	2566.8
	Rutledge/ Southern Red Hills district of the East Gulf Coastal Plain	1	6.2	3.4	11.2	19.1	795.8
Pike Co. Alabama	Ala. Hwy. 10/ Southern Red Hills district of the East Gulf Coastal Plain	2	5.6	2.2	51.6	76.2	1154.5
	Pike County Lake/ Southern Red Hills district of the East Gulf Coastal Plain	3	6.4	4.5	124.4	374.4	2914.2
	Sandy Run Creek/ Southern Red Hills district of the East Gulf Coastal Plain	2	6.7	3.4	57.2	208.5	1378.6
	Tick Hill/ Southern Red Hills district of the East Gulf Coastal Plain	2	5.8	2.2	62.8	137.9	1367.4
	Whitewater Creek/ Southern Red Hills district of the East Gulf Coastal Plain	2	6.6	2.2	56.0	170.4	1053.6

Bullock Co. Alabama	Bread Tray Hill/ Chunnenuggee Hills district of the East Gulf Coastal Plain	2	4.6	9.0	105.4	57.2	683.7
Webster Co. Georgia	Plains/ Fall Line Hills district of the East Gulf Coastal Plain	4	7.8	29.1	195.0	544.7	14503.8
Jefferson Co. Alabama	Leeds/ Cahaba Valley district of the Alabama Valley and Ridge	4	8.0	59.4	123.3	764.4	37750.3
	Turkey Creek/ Cahaba Valley district of the Alabama Valley and Ridge	3	7.6	13.5	28.0	527.9	3754.9
Shelby Co. Alabama	Hwy. 107/ Cahaba Valley district of the Alabama Valley and Ridge	3	7.9	5.5	264.5	1423.5	7218.3
	Ebenezer Church/ Cahaba Valley district of the Alabama Valley and Ridge	3	7.8	11.2	70.6	1125.3	7621.8
Blount Co. Alabama	Blountsville/Sand Mountain district of the Cumberland Plateau	3	5.8	4.5	152.4	192.8	8305.5

* 1. Sandy Soils. 2. Loams and Light Clays. 3. Clays and soils high in organic matter. 4. Clays of the Black Belt.

III. POLLINATION BIOLOGY, ACHENE DISPERSAL, AND RECRUITMENT

INTRODUCTION

The southeastern region of the United States is an area of high biological diversity, containing many endemic plant species (Estill and Cruzan 2001, Ricketts *et al.* 1999, Flather *et al.* 1998, Dobson *et al.* 1997, Gentry 1986, Kral 1983). The Atlantic and Gulf Coastal Plain Floristic Province ranks second in the number of endemic species of floristic regions in North America north of Mexico (Sorrie and Weakley 2001). Many of these endemics are also rare within the region, making them vulnerable to extinction (Estill and Cruzan 2001). One such species is *Rudbeckia auriculata* (Perdue) Kral (Asteraceae), which is listed as globally imperiled by both the Alabama and Georgia Natural Heritage Programs (Alabama Natural Heritage Program 2004, Georgia Natural Heritage Program 2004).

Extensive surveys by several individuals conducted over a 20-year period have failed to document substantial numbers of new populations of *R. auriculata* (Diamond and Boyd 2004, Schotz 2000, Kral 1983, McDaniel 1981). Sites apparently appropriate for *R. auriculata* (i.e. wet, sunny, disturbed areas such as roadsides, power line corridors and the edges of beaver ponds) occur between known populations, and often support commonly associated species (Diamond and Boyd 2004). *Rudbeckia auriculata* occurs on a wide range of soils and does not seem to be restricted by this factor (Diamond and

Boyd 2004). The general rarity of *R. auriculata*, but local abundance at certain sites, suggests that one or more factors limit population size and dispersal of this species. Among possible factors are lack of pollinators, poor achene set, poor achene dispersal, low germination rates, and poor seedling recruitment (Schotz 2000).

Previous reports on *R. auriculata* have provided limited information on potential pollinators (Schotz 2000). If pollinators are restricted to a few insect species, particularly if these species are rare or declining, pollination and seed set could be major limiting factors. Pollinator declines, especially of native bees, have been documented due to such factors as loss or modification of habitat, competition with non-native species, and pesticide use (Kearns and Inouye 1997). Maintenance of ecosystem integrity requires preservation of both plants and their pollinators (Tepedino *et al.* 1997). *Rudbeckia auriculata* is a wetland-associated species, and over half of this habitat in Alabama has been lost since 1780 (New Mexico Center for Wildlife Law 2003). Habitat fragmentation or loss can lead to the local extinction of insects that may be significant pollinators of native plants and could further jeopardize rare species, especially if they are dependent on specialist pollinators (Kearns *et al.* 1998, Rathcke and Jules 1993, Saunders *et al.* 1991).

Among the tools potentially available for the management of rare plant species are the establishment of new populations on protected sites and the augmentation of existing natural populations with propagated plants. The U. S. Fish and Wildlife Service supports “the controlled propagation of listed species” and calls for “supporting recovery related research, maintaining refugia populations, providing plants or animals for reintroduction or augmentation of existing populations, and conserving species or populations at risk of imminent extinction or extirpation" (U. S. Fish and Wildlife Service 2003b). However, detailed studies of seed germination and seedling establishment requirements of many plant species are unavailable (Schemske *et al.* 1994, Menges 1986). Information on seed and seedling biology is especially scarce for many native species due to the narrow windows of opportunity for observing these events coupled with the often rare or ephemeral nature of sites suitable for seedling establishment in nature (Schulze *et al.* 2002). Previous reports on *R. auriculata* have provided limited information on these topics (Schotz 2000). Therefore, any contributions to our knowledge of achene dispersal and seedling ecology would increase management options for *R. auriculata.*

The questions that this study was designed to answer are: (1) What are the main pollinators of *R. auriculata*?; (2) Is insect visitation required for achene production?; (3) Do significant differences exist in achene production among populations of various sizes?; (4) What is the rate of achene dispersal in *R. auriculata*?; and (5) Do disturbance and the reduction of competition affect seedling recruitment of *R. auriculata*?

METHODS

Study species

Rudbeckia auriculata is a member of the composite tribe Heliantheae (Cronquist 1980). It is characterized by sticky masses of pollen rarely disturbed by shaking or wind, and receptive stigmas located near the disc petals in a position easily contacted by insects (Dickinson and McKone 1992). Heads are numerous in open panicles, with bright orange-yellow ray flowers and conical purplish-black disc flowers. Disc flowers open in early morning, and the bright yellow pollen is easily visible. Despite being conspicuous members of the flora, little information exists on the floral visitors of members of this tribe (Dickinson and McKone 1992). The flowering period for *R. auriculata* throughout its range is late July through early November, with most plants finished by September (Diamond pers. obs.). Ray flowers are neutral (containing neither fertile stamens nor pistils), and each disc flower has a single ovule. Achenes (fruits) are purplish-brown, with four to six small teeth at the apex (Fig. 1) (Schotz 2000, Kral 1983, 1975), and mature in October (Diamond pers. obs.).

Study sites

Thirty-two populations of *R. auriculata* have been reported in three southeastern states: Alabama (30), Florida (1), and Georgia (1) (Diamond and Boyd 2004). Of this number, six have been extirpated (Diamond and Boyd 2004). Although a few sites support over 1,000 flowering stems, 19 support 50 or fewer flowering stems (Schotz 2000, Diamond and Boyd 2004). Eight Alabama populations that represent diverse population sizes as well as geographic locations within the range of the species were chosen as study sites (Table 1). Size categories were chosen based upon the size range of populations available for study.

Floral visitors and pollen loads

To determine the main pollinators of *R. auriculata*, insect visitors were collected during peak flowering from 1999 to 2002 (Table 1). I collected insects from five sites in 1999, two sites in 2001, and one site in 2002. A minimum of five collecting trips were made to each site. Each visit was a one-hour period, and trips were evenly distributed through the day (*i.e.* 2 morning, 1 midday, 2 evening). No insects were observed on the flowering heads of *R. auriculata* during nine survey trips to different populations between sunset and midnight (Diamond pers. obs.). As a result, I conducted all subsequent visitor studies during daylight hours.

Insects were collected with a standard entomology net while on flowering heads of *R. auriculata*. They were later separated into taxonomic groups for further identification and characterization of pollen load. Identifications were made to the family level (Borror *et al.* 1989) and voucher specimens were accessioned into the Troy University entomology collection. The total number of insects collected at a site was divided by the total number of collecting hours at that site to calculate a Catch Per Unit Effort (CPUE) value. Each insect was examined under10X magnification to assess pollen load. *Rudbeckia* pollen grains are bright yellow in color, have numerous spines on their surface, and are approximately 20 µm in diameter (Fig. 2). Nine locations on each insect were examined: top of head, bottom of head, top of thorax, bottom of thorax, top of abdomen, bottom of abdomen, legs and feet, proboscis, and corbiculae (if present). The pollen load of each area was assigned a relative numerical value based upon the amount of pollen present: 3 = dense (more than 1,000 grains), 2 = moderate (100-1,000 grains), 1 = scattered (less than 100 grains), and 0 = no pollen. An overall estimation of pollen load was assigned to each insect utilizing the same four categories. A mean Pollen Load Index (PLI) value was calculated by dividing the total pollen load for each species at each site by the total number of individuals of that species collected at the site.

To identify *R. auriculata* pollen removed from captured insects, anthers of *R. auriculata* and associated flowering species were collected to form a reference pollen collection. Species whose flowering period at least partially over-lapped that of *R. auriculata* included *Helianthus angustifolius* L., *Helenium autumnale* L., *Vernonia* *gigantea* (Walt.) Trel., *Ipomoea coccinea* L., and *Clematis virginiana* L. Pollen samples were removed from twenty insects chosen arbitrarily from each of the three most important families of visitors (Andrenidae, Megachilidae and Halictidae), where importance was based upon insect abundance and pollen load. Six areas on each insect were sampled utilizing individual 2 mm^2 glycerin gel squares: face, top of thorax, bottom of thorax, top of abdomen, bottom of abdomen, and legs/feet. The gel was affixed to a slide and examined under 40X magnification. Pollen grains were identified utilizing the reference pollen collection.

Due to a low sample size and the inability to test for normality, a Spearman's correlation value was calculated between CPUE and the number of flowering stems at each site to determine if larger populations attracted more insect visitors. A Kruskal-Wallis test was used to determine if there were differences in the numbers of individuals of certain insect families collected at populations of different sizes (Conover 1971).

I further identified periods of peak insect activity by collecting floral visitors during hourly time blocks from 7 a.m. until dark at the Florala site. Sampling was conducted on six rain free days in 2001 (August 1st-4th, August 10th, and August 15th). This site was chosen as representative of medium to large sized populations. The mean number of insects collected per hour from 7 a.m. until darkness was tabulated.

Achene Set

To ascertain if insect visitation was required for achene production, I conducted a pollinator-exclusion experiment. I bagged 40 flower heads on five potted plants (8 heads per plant) located at my home in Pike County, Alabama. The entire head was enclosed in a fine mesh nylon bag (625 holes/645.2 mm^2). Heads were bagged while individual flowers were still in tight bud. After the heads matured in late October, achenes were opened with forceps and visually inspected. If no embryo was present or if the embryo was severely shrunken or discolored as compared to a normal embryo for this species, the achene was considered inviable.

Achene set in natural populations was determined by arbitrarily collecting 10 heads from each of five sites: two with large numbers of plants (Rutledge and Florala), one with a medium number of plants (White Water Creek), and two with low numbers of plants (Hwy. 10 and Buck Creek) in October of 1999, after the achenes were mature but before dispersal began. Heads were collected from different flowering stems at all sites except Buck Creek, where only three flowering stems were produced. Achenes were examined and classified as mature or inviable utilizing the same procedures as in the pollinator exclusion study. Achenes damaged by insects were assumed to have contained viable embryos. A Kruskal-Wallis test was performed to determine if there were significant differences in mature achene production among populations of various sizes.

Achene dispersal

During 2000-2001, three potted plants were individually staked in an upright position on the center of a white sheet (2.7 m x 2.6 m), one plant per sheet, in an open grassy area at the author's home. The sheets were checked daily from 1 October 2000 until 28 February 2001 for achenes. The dispersal distance for each achene from the center of the pot was measured and the achene removed. Because there was little wind movement at ground level, and because achenes have little pappus, it is unlikely movement occurred after they landed (Diamond pers. obs.).

Recruitment

Rudbeckia auriculata requires some form of disturbance and favors open sunny sites, such as roadsides and power line right-of-ways, where plants are subjected to mowing as well as flooding (Schotz 2000, McDaniel 1981). To determine the effects of disturbance on seedling establishment and survival I collected mature achenes from the Rutledge population in early October 2001, and arbitrarily divided them into batches of 50 each. Three field plantings and one control (with five replicates each) were undertaken in February 2001. In the control, 50 achenes were scattered on the soil surface of 3.8 L plastic nursery pots filled to within 2.5 cm of the lip with standard potting soil. Pots were located in a sunny outdoor location (Pike County, Alabama) and placed in water filled pans to provide constant soil moisture. The achenes were not covered with soil. Seedlings were flagged upon emergence with small wooden stakes, and the number of surviving seedlings was tallied in each pot.

Field plantings were located at the confluence of Beeman and Mill Creeks in Pike County, Alabama. *Rudbeckia auriculata* is not known to occur upstream in the watersheds of either creek, and thus no contamination could occur from achenes washed down stream. Based upon germination studies, achenes of this species lose viability rapidly after dispersal (Diamond pers. obs.), and no soil seed bank could be present. Achenes were scattered onto 15 square plots, each 0.3 meters in size on each side. Three treatments were assigned randomly to the plots: (1) the vegetation was clipped at soil level but the clippings were not removed to simulate mowing (Clipped Not Removed: CNR); (2) the vegetation was clipped at soil level and the clippings removed to simulate flooding after mowing (Clipped Removed: CR); or (3) the vegetation was clipped at the soil surface, the clippings and leaf litter removed, and the soil was then disturbed with a garden rake and any noticeable roots removed to a depth of 10 cm to simulate severe scouring during flooding (Clipped Removed Disturbed: CRD). Seedlings were flagged upon emergence with small plastic stakes, and the number of surviving seedlings was tallied in each plot. Results were analyzed by a one-way Analysis of Variance (ANOVA) to determine if there was a significant difference in survivorship among the treatments at the end of the study. The Student-Newman-Keuls test was utilized to determine which treatments, if any, significantly differed. All statistical analyseis was performed using SPSS 11.5 for Windows with $\alpha = 0.05$.

RESULTS

Pollinators and Pollination Mechanisms

What are the main visitors of *R. auriculata*? The most common insect species collected was a composite specialist bee, *Andrena aliciae* Robertson, which accounted for 50% of total visitors. Four hundred and sixty-six individuals representing five insect orders and 17 families were collected during this study (Table 2). The most frequently collected families were Andrenidae, Megachilidae, and Scoliidae, which accounted for 84% of total visitors.

Larger populations of *R. auriculata* attracted more floral visitors (CPUE vs number of flowering stems, Spearman's rank test, rho = 0.842, $p = 0.009$, $N = 8$). Large and medium sized populations attracted more Andrenids and Megachilids than small populations ($X^2 = 6.23$, df = 2, $p = 0.033$ for Andrenids and $X^2 = 6.81$, df = 2, $p = 0.044$ for Megachilids). Insect visitors of *R. auriculata* differed in the quantity of pollen they transported (Table 3). Samples from Andrenid, Megachilid, and Halictid bees revealed only *R. auriculata* pollen. Greatest insect activity on *R. auriculata* heads was in early morning (8-10 a.m.) at the Florala site, shortly after the dew dried, with a second smaller peak late in the afternoon (5 p.m.) (Fig. 3).

Achene Set

Is insect visitation required for achene production, and do significant differences exist in achene production among populations of various sizes? The mean percentage of filled achenes in bagged heads was 2.1% per head. Mean proportion of filled achenes per head in unbagged heads at sampled populations were 31.4% for Rutledge, 26.5% for Florala, 29.2% for White Water Creek, 16.9% for Hwy. 10, and 0.24% for Buck Creek. A Kruskal-Wallis test determined that larger populations produced more filled achenes ($X^2 = 20$, df = 3, $p < 0.001$).

Dispersal Distance

What is the distance of achene dispersal in *R. auriculata*? Eighty-two percent of the achenes from plants staked on sheets had been recovered by 1 December. The majority of achenes (72%, N = 1395) fell within 0.3 meters or less of the center of the pot, with a rapid decline as distance increased from plants (Table 4).

Seedling recruitment

Does disturbance and the reduction of competition affect seedling recruitment of *R. auriculata*? No seedlings emerged in plots where the vegetation was clipped but not removed. After five months, the treatment with vegetation clipped and removed and soil disturbed (CRD) and the treatment with vegetation clipped and removed but no soil disturbance (CR) had 74.6% and 12.7% of the mean control survivorship, respectively (Table 5). Levene's test for homogeneity of variances showed that the three remaining treatments had approximately equal variances, and Q-Q plots showed that the data did not differ significantly from normality. Hence, ANOVA was used and revealed a significant difference in survivorship for the July measurements (F = 17.9, df = 2, 12, $p < 0.001$). Using a Student-Newman-Keuls multiple comparison test, the CRD treatment and the control were not significantly different ($p > 0.05$), and the CR treatment was significantly different from both the CRD treatment and the control ($p < 0.05$).

DISCUSSION

Pollinators and Pollination Mechanisms

Andrena aliciae, which accounted for 50% of total visitors to *R. auriculata,* has been associated with other *Rudbeckia* species, including *R. hirta* L., *R. laciniata* L., and *R. triloba* L. (Hilty 2003). The floral visitors of *R. hirta* in a Minnesota prairie remnant were reported to be mostly (90%) *Andrena* bees (Dickinson and McKone 1992).

Some previous researchers have found no correlation between the abundances of floral visitors and their effectiveness as pollinators (Olsen 1997, Pettersson 1991, Herrera 1987, Montalvo and Ackerman 1986, Sugden 1986). However, based upon my observation of pollen load (Table 3), and upon achene set at populations where *Andrena aliciae* was present versus those where it was not observed, *A. aliciae* is likely an important pollinator in medium and large populations of *R. auriculata.*

Scoliidae represented 11% of total collections. Adults are often associated with flowers (Borror *et al.* 1989) and have been reported as potential pollinators of other plant species (Landeck 2002, Clardy *et al.* 2001). However, I do not consider them important pollinators of *R. auriculata* as 86% of the individuals examined (N = 51) carried no pollen (Table 3). Halictids were present at all but one site, but were a notable proportion of floral visitors only at the Turkey Creek site, where they were 72% of visitors collected. At that site they appeared to be the major transporters of *R. auriculata* pollen based upon pollen load (Table 3).

Seventeen of the twenty Nymphalid records were Pearl Crescent butterflies (*Phyciodes tharos* Drury). This species is reported as a visitor to other *Rudbeckia* species, including *R. hirta* L., *R. laciniata* L., and *R. triloba* L. (Hilty 2003). Early (1988) reported that this species preferentially visited flowers with a floral pattern (shape, color) characteristic of *R. hirta*, and that flower visitation was poorly correlated with flower density and frequency. This species was the only visitor observed at the Hwy. 10 site, a small population consisting of only 10 flowering stems. However, only three of these butterflies had any *Rudbeckia* pollen on their bodies and then only a few grains each. Thus, this species is unlikely to be an effective pollinator.

Schotz (2000) reported several types of insects visiting *R. auriculata,* including honey bees, bumblebees, syrphid flies, and various butterflies, and stated that *R. auriculata* did not appear to attract specific pollinators. Introduced honey bees (*Apis mellifera* L.) were neither observed nor collected on *R. auriculata* during my study. The Andrenid bees superficially resemble honey bees, and may have been mistaken for them by Schotz (2000) when observed at a distance.

Microscopic examination of pollen samples removed from twenty Andrenid, Megachilid, and Halictid bees revealed only *R. auriculata* pollen. These insect species seem to demonstrate a high fidelity for *Rudbeckia* inflorescences, since other species, including other composites, were also blooming within the study areas.

In general, pollinators are more attracted to large floral displays than to small ones (Goulson *et al.* 1998, Stout *et al.* 1998, Kunin 1993). In addition, some types of pollinators exhibit density-dependent foraging behavior and may bypass small populations (Lamont *et al.* 1993). Several studies have demonstrated that an increased floral display increases the number of pollinator visits (Kawarasaki and Hori 1999, Conner and Rush 1996, Klinkhamer *et al.* 1989). This seems to be the case in this study, as I found a significant positive correlation between CPUE and the number of flowering stems. There was also a noticeable downward trend in the number of individuals of Andrenid and Megachilid bees (two of the most important pollinators) with decreased population size (Table 2). Schmalhofer (2001) demonstrated that not only did larger patches of flowers attract more pollinators, but the sizes of these pollinators were also greater in larger patches. This was the case in my study also, as the Andrenid and Megachilid bees were among the largest floral visitors I observed.

Insect activity often varies diurnally (Neff and Simpson 1990, Simpson and Neff 1987). There were two periods of high visitor activity for *R. auriculata* at the Florala site. Dickinson and McKone (1992) reported high visitation rates early in the day. They bagged heads of *Ratibida pinnata* (Vent.) Barnh. (Asteraceae: Heliantheae) and removed the bags at 8:45 a.m. the next day. By noon, most of the pollen had been removed (Dickinson and McKone 1992). In *Helianthus annuus* L., a second afternoon peak of insect visitation has also been reported (Neff and Simpson 1990, Simpson and Neff 1987, Hurd *et al.* 1980). In my study, the bee species in particular favored sunny weather or open areas, avoiding plants in the shade and disappearing on cloudy days, perhaps due to lower temperatures (Diamond pers. obs.). This fact may account for the low numbers of

Andrenid bees at the Patsaliga site (Table 2), which bordered a hardwood forest and was in shade for much of the day. Two distinct periods of foraging behavior have been reported in other bee species, and may be related to temperature, illumination, competition, predation, or physiological traits (Gottlieb *et al.* 2005, Willmer 1988, Gerling *et al.* 1983). It is not known which factor(s) may have influenced activity in this Andrenid species.

Achene Set

Many plant species are dependent upon insect pollination for seed production (Real 1983). This study indicates that *R. auriculata* heads require insect visits for achene set. There was low production of filled achenes in *R. auriculata* heads bagged with insect-excluding mesh, although some pollen was observed on the stigmas of bagged heads. Upon dissection, mean percent achene set was 2.1% per head. Florez and McDonough (1974) reported a mean of 3% filled achenes in bagged capitula of *Rudbeckia occidentalis* Nutt. during a study of that species in Utah. Many other species of Asteraceae have also been demonstrated to be self-incompatible or only partially self-compatible (Costin *et al.* 2001, Giblin and Hamilton 1999, Kawarasaki and Hori 1999, Messmore and Knox 1997, Olsen 1997, Leuszler *et al.* 1996, Byers 1995, Buchele *et al.* 1992, Andersson 1991). This fact alone, however, does not explain *R. auriculata*'s restricted distribution. Numerous other self-incompatible species of Asteraceae are widespread and even weedy in nature (Gross and Werner 1983, Havercamp and Whitney 1983, Mulligan and Findlay 1970, Fryxell 1957). Karron (1987) in fact states that there was “no significant difference in the levels of self-incompatibility of restricted and widespread species…” after a study of species in ten genera.

Data on mean total achene production from the naturally occurring populations of *R. auriculata* in 1999 varied from a high of 31.4% to a low of 0.24%. This is within the range of achene set in open pollinated flowers of *Solidago* species (Asteraceae) as reported by Gross and Werner (1983). Analysis demonstrated that achene set did not differ between large and medium populations, but achene set in small populations was significantly less. This supports the premise that *R. auriculata* in small populations is pollinator-limited, failing to attract the bee species which are the main pollinators in larger populations. Reduced seed production in small populations due to a lack of pollinators has been reported for other plant species (Oostermeijer *et al.* 1998, Pettersson 1996, Johnson *et al.* 1995). Plants in small populations may also be subjected to higher rates of self-pollination or receive pollen from closely related siblings, both of which can decrease seed production (Byers 1995, Lamont *et al.* 1993, Jennersten 1988a). Observation of pollinators in the field suggests that they move more often between heads on the same flower stalk than between heads on different flower stalks (Diamond pers. obs.). The Buck Creek population had a lower mean achene set than the mean achene set for bagged heads (0.24% vs. 2.1%). This may be due to the extremely small size of this population (2 flowering stems). Low rates of pollinator visitation, along with a low level of self-compatibility, may place small populations at risk of extirpation (DeMauro 1993), and should be taken into consideration when developing conservation plans for this species.

Dispersal Mechanisms

Schotz (2000) stated that the achenes of *R. auriculata* are likely too small to serve as food for any wildlife species, and lack any apparent adaptations for long-distance dispersal. The teeth on the achene appear too short and too weak to adhere firmly to an animal's fur, and dispersal appears to be highly localized, relying on gravity. Gravity has been reported as the dispersal mechanism for *R. occidentalis* (Florez and McDonough 1974). For *R. auriculata*, observations in 1999-2000 on marked heads in natural populations support the premise that gravity is the primary dispersal agent. No vertebrate animals were observed feeding on the achenes during observations, and marked heads did not exhibit any obvious damage from possible nocturnal seed predators. The heads slowly shed the achenes and broke apart from bottom to top over time.

The achene dispersal distance study also supports the premise that gravity is the primary dispersal agent. Heads began to shed mature achenes in October, and most had been released by January. Most recovered achenes (72%) fell within 0.3 meters or less of the center of each pot, with a rapid decline in numbers of achenes as distances increased. Florez and McDonough (1974) reported that 56% of dispersed achenes of *R. occidentalis* fell within 0.9-1.6 meters of marked stems of that species. However, for *R. auriculata* secondary dispersal by water (hydrochory) may be significant. When placed in water the achenes remain bouyant for extended periods of time (more than a month) and can even germinate while floating (Diamond, pers. obs.). All known populations of this species occur in wetland habitats, often near flowing water and are frequently subjected to flooding (Diamond and Boyd 2004). Secondary hydrochory may be the primary means of long distance dispersal in this species. Several sets of populations occur near each other on the same stream or on feeder streams: Red Level and Buck Creek; Florala and Richland Creek; Gin Creek and Rutledge; Patsburg, Mill Creek and Patsaliga River;

Leeds, Leeds 1 and Leeds 2; Sandy Run and Hwy. 10; Ebenezer Church, Hwy. 7, Hwy. 22 and Dirt Road (Diamond and Boyd 2004).

Seedling recruitment

Schotz (2000) suggested that germination and establishment is rather poor in *R. auriculata,* based on field inspections for seedlings. In over 10 years of field observations, the author has yet to find a seedling in the field. As most of the populations occur on roadside or power line right-of-ways that are mowed, there is often a large amount of plant litter on the soil surface. In my seedling recruitment study, no seedlings emerged in plots that had the vegetation clipped but not removed. Thick mats of litter like those produced by mowing most likely prevent the lightweight achenes of *R. auriculata* from reaching the soil surface and conditions favorable for germination. After five months, plots with vegetation clipped, litter removed and soil disturbed (CRD treatment), and plots with vegetation clipped, litter removed but without the soil disturbed (CR treatment), had 74.6% and 12.7% of the control survivorship respectively (Table 5).

Figure 1: Drawing of *Rudbeckia auriculata* achene.

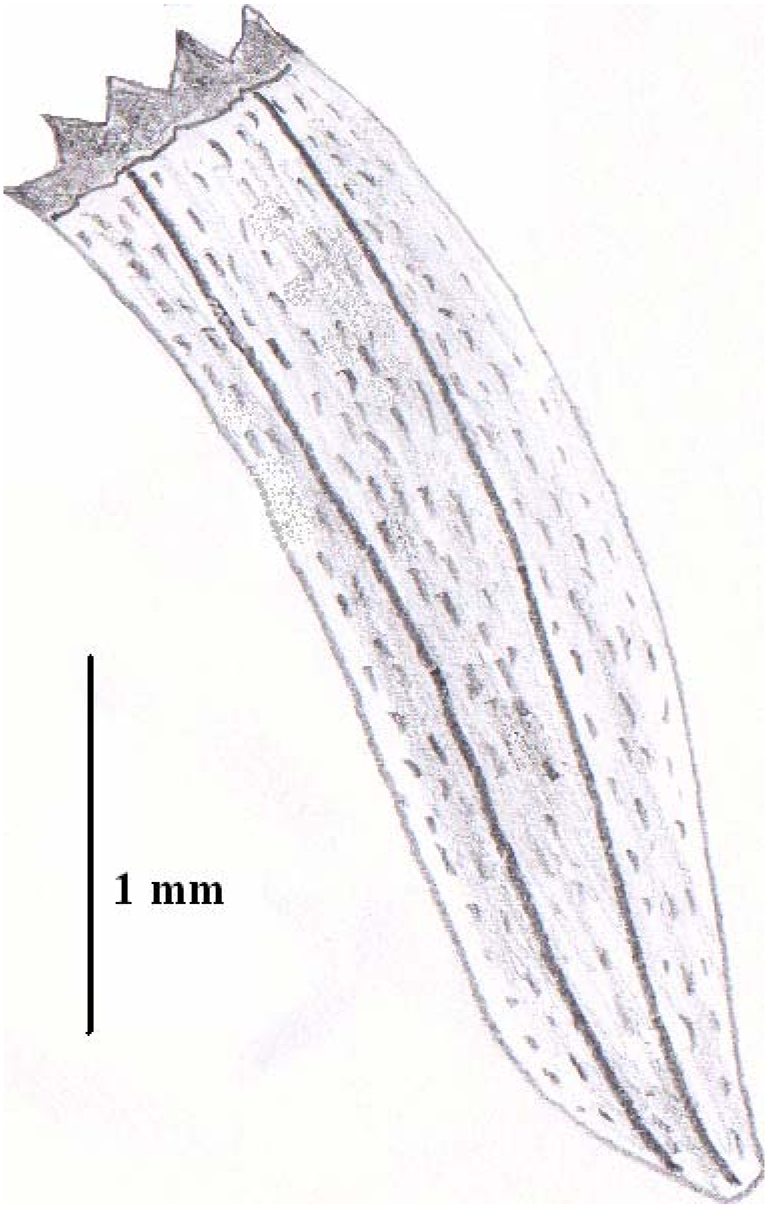

Figure 2: Pollen grains of *Rudbeckia auriculata*.

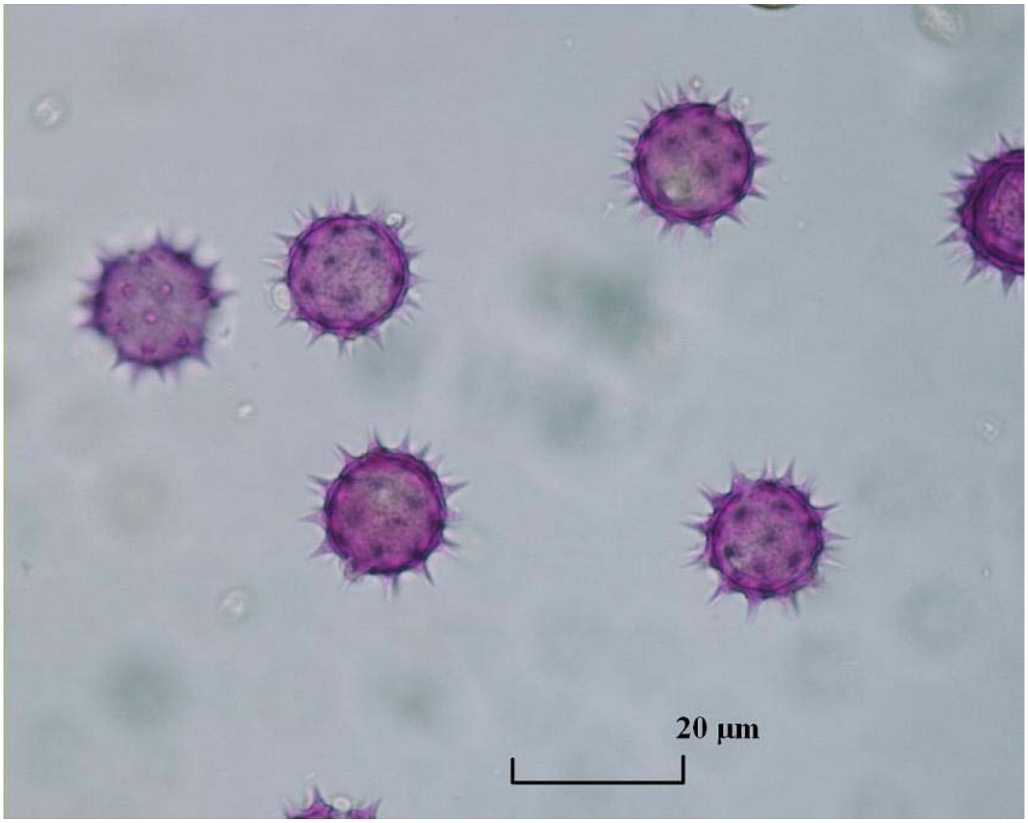

Figure 3: Mean number of insects collected per hour from 7 am until darkness at the Florala site August 1st-4th, August 10th, and August 15th 2001.

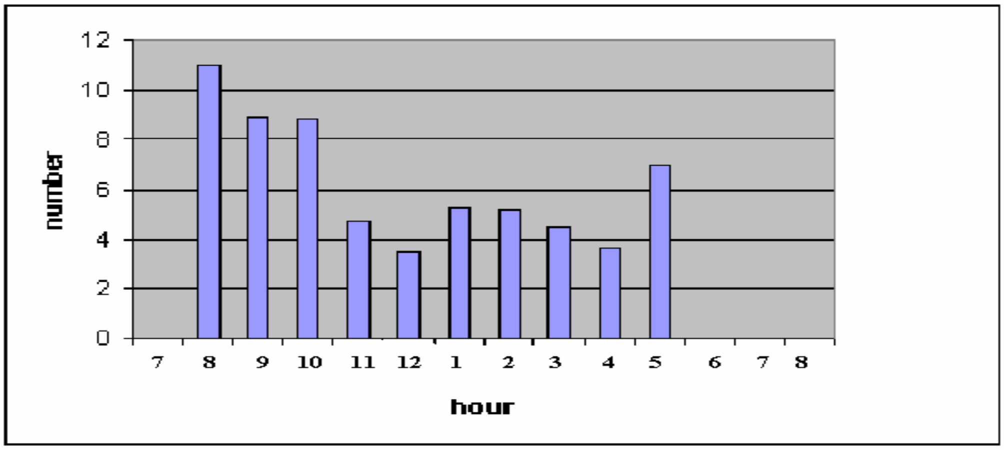

Table 1: Study sites listed by population size (large: 1000+ flowering stems; medium: 40-999 flowering stems; small: < 40 flowering stems). Physiographic provinces from the Cartographic Research Laboratory (1975).

County	Site Name/ Location	Physiographic provinces	Population Size	Year data collected	Habitat Description
Covington Co. Alabama	Florala/ 31° 02' 23"N, 86° 13' 07"W - HACODA quad	Dougherty Plain District, East Gulf Coastal Plain	Large	2002	Roadside and disturbed area near a small stream
Crenshaw Co. Alabama	Rutledge/ 31° 43' 41"N, 86° 19' 32"W - LUVERNE quad	Southern Red Hills District, East Gulf Coastal Plain	Large	1999	Power line right of way near a beaver pond.
Crenshaw Co. Alabama	Patsaliga River/ 31° 43' 36"N, 86° 16' 52"W - LUVERNE quad	Southern Red Hills District, East Gulf Coastal Plain	Medium	1999	Roadside near a beaver pond.
Pike Co. Alabama	White Water Creek/ 31° 44' 37"N, 85° 51' 41"W - BRUNDIDGE quad	Southern Red Hills District, East Gulf Coastal Plain	Medium	1999	Roadside along a small creek.
Jefferson Co. Alabama	Turkey Creek/ 33° 41' 57"N, 86° 40' 21"W - PINSON quad	Cahaba Valley District, Alabama Valley and Ridge	Small	2001	Around a spring complex and beaver pond on a small stream.
Shelby Co. Alabama	Ebenezer Church/ 33° 09' 55"N, 86° 48' 41"W - ALABASTER quad	Cahaba Valley District, Alabama Valley and Ridge	Small	2001	Edge of a beaver pond.
Pike Co. Alabama	Hwy. 10/ 31° 43' 32"N, 85° 45' 56"W - BRUNDIDGE quad	Southern Red Hills District, East Gulf Coastal Plain	Small	1999	Roadside at the edge of a beaver pond.
Covington Co. Alabama	Buck Creek/ 31° 25' 02"N, 86° 35' 00"W - RED LEVEL quad	Dougherty Plain District, East Gulf Coastal Plain	Small	1999	Roadside edge of an old beaver pond.

Table 2: Insect orders, families, and numbers of individuals collected on *Rudbeckia auriculata* flowering heads for each site. Collection sites: 1 = Florala; 2 = Rutledge; 3 = Patsaliga; 4 = White Water Creek; 5 = Turkey Creek; 6 = Hwy. 10; 7 =Buck Creek; 8 = Ebenezer.

Collection Site	1	2	3	4	5	6	7	8	Totals
Insect Orders (in bold) and Families	Number								
Hymenoptera									87.9%
Andrenidae	183	17	5	29					234
Anthophoridae	1	2		2					5
Apidae	6			1	4				11
Halictidae	3	1	3	1	23				31
Ichneumonidae	1								1
Megachilidae	54	2	1	1					58
Scoliidae	47	4							51
Sphecidae	3	1							4
Vespidae	14	1							15
Diptera									6.4%
Muscidae	1								1
Syrphidae	26				3				29
Lepidoptera									4.9%
Hesperiidae				2					2
Nymphalidae		8	3	6	1	2			20
Zygaenidae		1							1
Coleoptera									0.4%
Cantharidae			1						1
Mordellidae					1				1
Hemiptera									0.2%
Lygaeidae	1								1
Totals	340	37	13	42	32	2	0	0	466

Table 3: Insect orders and families collected on *Rudbeckia auriculata* flowering heads, with Catch Per Unit Effort (CPUE) and Mean Pollen Load (MPL) index values. MPL values range from 3 (dense pollen load) to 0 (no pollen).

Collection Site								
	Florala	Rutledge	Patsaliga	Pike 231	Turkey Creek	Hwy.10	Buck Creek	Ebenezer
Insect Orders (in bold) and Families	CPUE/ MPL	CPUE/ MPL	CPUE/ MPL	CPUE/ MPL	CPUE/ MPL	CPUE/ MPL	CPUE /MPL	CPUE/ MPL
Hymenoptera								
Andrenidae	4.6/2.9	2.1/2.4	0.8/3	4.1/2.3				
Anthophoridae	0.02/3	0.3/1		0.3/2.5				
Apidae	0.2/1			0.1/2	0.5/1			
Halictidae	0.1/2	0.1/2	0.5/2	0.1/2	2.9/1.2			
Ichneumonidae	0.02/0							
Megachilidae	1.4/2.9	0.3/1.5	0.2/2	0.1/1				
Scoliidae	1.2/0.1	0.5/1.3						
Sphecidae	0.1/1.3	0.1/1						
Vespidae	0.4/0	0.1/0						
Diptera								
Muscidae	0.02/0							
Syrphidae	0.7/0.8				0.4/0			
Lepidoptera								
Hesperiidae				0.3/0				
Nymphalidae		1/0.4	0.5/0	0.9/0	0.1/0	0.3/0		
Zygaenidae		0.1/0						
Coleoptera								
Cantharidae			0.2/1					
Mordellidae					0.1/0			
Hemiptera								
Lygaeidae	0.02/0							
Total insects	340	37	13	42	32	2	0	0
Hours of collection time	43	8	6	7	8	6	5	5
Total site CPUE	7.9	4.6	2.2	6	4	0.3	0	0

Table 4: Achene dispersal distance from the center of the pot for three staked plants over time.

Distance								
Month		0.3 m or less	0.3-0.6 m	0.6-0.9 m	0.9-1.2 m	1.2-1.5 m	Over 1.5 m	Total #
October		324	137	29	7	5	0	502
November		511	87	11	21	5	2	637
December		108	31	18	3	1	1	162
January		43	13	8	1	3	0	68
February		20	3	1	1	0	1	26
Total #		1006	271	67	33	14	4	1395
%		72 %	19 %	5 %	2 %	1 %	0.3 %	100 %

Table 5: Mean monthly survivorship of field planted *Rudbeckia auriculata* in 2001 under each of three treatments and percent of control survivorship.

Treatment	March	% of control	April	% of control	May	% of control	June	% of control	July	% of control
1: Achenes in pots (Control)	26.4	100	25.6	100	24.6	100	22.8	100	22.0	100
2: Vegetation clipped, litter not removed (CNR)	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0
3: Vegetation clipped, litter removed (CR)	13.0	49.2	7.8	30.5	5.6	22.8	3.6	15.8	2.8	12.7
4: Vegetation and litter removed, soil disturbed (CRD)	23.0	87.1	20.2	78.9	18.2	74.0	17.6	77.2	16.4	74.6

IV. *RUDBECKIA AURICULATA* INFECTED WITH A POLLEN-MIMIC FUNGUS IN ALABAMA

INTRODUCTION

Fungi that alter floral parts or vegetative portions of plants to resemble flowers (pseudo-flowers) and the insects that act as vectors for their spores have been reported for many species of plants. Insect pollinators have been identified as agents of dispersal for fungal pathogens in *Silene* (Soldatt and Vetter 1995, Thrall *et al.* 1993; 1995, Antonovics and Alexander 1992, Real *et al.* 1992, Alexander 1990, Baker 1947), several species of Cruciferae (Roy 1993, 1996), *Euphorbia cyparissias* L. (Pfunder and Roy 2000), and members of the Ericaceae (Batra 1987; 1991, Batra and Batra 1985). This relationship may be quite common (Roy 1996).

Perhaps the most familiar case of floral mimicry is that of the rust *Puccinia monoica* (Peck) Arth., which infects species of crucifers and grasses (Roy 1993, 1994, 1996). The fungus prevents the infected host plant from flowering, and causes it to produce pseudo-flowers from vegetative tissues that resemble flowers of other species in size, color, shape, scent, and nectar production (Roy 1993). Species of *Ustilago* infect at least 92 species of caryophyllaceous plants in Europe and 21 in North America (Delmotte *et al*. 1999, Skykoff and Bucheli 1995, Soldaat and Vetter 1995, Skogsmyr 1993, Thrall *et al.* 1993), rendering the plants sterile the next season when fungal spores are produced instead of pollen (Skogsmyr 1993). In the genus *Vaccinium*, the fungus *Monilinia* infects flowers, fruits, and shoots. Infected tissues are ultraviolet reflective, fragrant, and produce sugar secretions that attract insects (Caruso and Ramsdell 1995). In all instances insect visitors to otherwise healthy plants spread the fungal pathogen.

During field work on investigations of insect pollinators of *Rudbeckia auriculata* (Perdue) Kral in 1999, a fungus was observed infecting flower heads at a site in Crenshaw County, Alabama (31° 43' 42" N, 86° 19' 33" W). In 2001, the same fungus was observed infecting flower heads at a second population located approximately 84 km to the south in Covington County, Alabama (31° 02' 23" N, 86° 13' 07" W). The fungus was identified by plant pathologists at Auburn University as *Fusarium semitectum* Berk. & Ravenel, a common soil fungus that infects many plant species worldwide (Singh *et al.* 1983, Marin-Sanchez and Jimenez-Diaz 1982, Nedumaran and Vidyasekaran 1982, Dhingra and Muchovej 1979). *Fusarium* species cause cereal ear blight in grain crops and have been reported to infect other species such as tobacco (*Nicotiana tabacum* L.), tomato (*Solanum lycopersicum* L.), soybean (*Glycine max* (L.) Merr.), and *Arabidopsis*, where disease symptoms were produced in anthers, filaments, and petals (Urban *et al.* 2002).

Fusarium semitectum produces orangish or pinkish-white spores that superficially resemble pollen on *R. auriculata* flower heads (Fig. 1). The appearance of infected flowers was similar to the appearance of *Fusarium* head blight on small grain crops (McMullen and Stack 1999). Individual flowers on which fungal spores developed did not produce pollen or achenes and were in effect sterile. The disc flowers of *R. auriculata* are dark purplish-black, and both the pollen grains and fungal spores were clearly visible. Upon closer inspection it was not difficult to distinguish the fungal spores from the golden yellow pollen. However, in the field, insects were observed to land on the infected heads and walk over them for short periods of time before flying to another head on the same or a different plant. Examination of pollen removed from insect visitors revealed fungal spores along with *Rudbeckia* pollen.

Rudbeckia auriculata flower heads infected with fungus were collected in 1999 to determine if the fungus could be transferred to healthy plants. The infected heads were lightly touched to heads of five individual potted plants located in Pike County, Alabama. The potted plants had been grown from achenes collected from populations in which the fungus had not been observed. Within 2-4 weeks the fungus was observed on most of the heads that had been exposed to the fungus.

Next I sought to determine: (1) if the fungus was present in the vegetative portions of stems below infected flowering heads, (2) the average fungal spore load and location of spores on the body of the most important floral visitor species, (3) the ratios of fungal spores to pollen grains on various areas of the body of the most important floral visitor species, and (4) the rate of spread of this pathogen.

Rudbeckia auriculata is listed as critically imperiled globally and critically imperiled within their states by the Alabama and Georgia Natural Heritage Programs (Alabama Natural Heritage Program 2004, Georgia Natural Heritage Program 2004). It is known from only one county in Georgia and 10 counties in Alabama, where populations are small and vulnerable to human disturbance (Diamond and Boyd 2004). Any agent responsible for decreased reproductive success could negatively impact this rare species.

METHODS

In order to determine if the fungus was present in vegetative portions of infected plants, entire stems with infected flowering heads were removed at ground level from the Crenshaw County site. The leaves and flowering heads were removed and the stems were washed with running water and surface sterilized by dipping for 2-3 minutes in 1% sodium hypochlorite in 10% ethanol. After rinsing with sterile water, the stems were cut into 5 mm longitudinal sections with sterile blades. These stem sections were placed in 100 ml sterile water and shaken vigorously for 1 minute. Afterwards, 0.5 ml of the dilution was spread on the selective medium, dichloran chloramphenicol peptone agar (DCPA; Burgess *et al.* 1988), which contains the growth retardant dichloran (Botran®), a chemical which delays the growth of other fungal genera but allows sporulation of *Fusarium* species, and chloramphenicol, an autoclavable antibiotic which prevents bacterial growth. *Fusarium* isolated by the above procedure were then grown on low nutrient medium Synthetischer Nährstoffärmer Agar (SNA) for identification. Fungal identifications were made utilizing the Synoptic FusKey *Fusarium* interactive key (Agriculture and Agri-Food Canada 2000) and keys by Burgess *et al.* (1988) and Nelson *et al.* (1983).

The most common insect species collected from *R. auriculata* was *Andrena aliciae* Robertson, which was also the principal pollinator, transporting a majority of the pollen (Diamond and Boyd 2004). Most other floral visitor species collected at the study site carried little or no pollen and were far less common (Diamond and Boyd 2004). For that reason we chose to focus this study on *A. aliciae*.

Collections were made at a study site in Crenshaw County where the fungus was present during peak flowering in 2002. *Andrena aliciae* bees were collected with a standard insect net while they were on flowering heads of *R. auriculata* that displayed no visible signs of fungal infection. Insects were captured, placed in a kill jar, and then transferred by forceps to individual vials. Vials were stored in a standard freezer. Pollen/fungal spore samples were removed from 20 bees chosen arbitrarily. Six areas on each bee were sampled utilizing individual 2 mm^2 glycerin gel squares: face, top of thorax, bottom of thorax, top of abdomen, bottom of abdomen, and legs/feet. The gel was affixed to a slide and the total numbers of pollen grains and fungal spores were counted for each sample area for each insect.

Correlation analysis was performed to determine if there were significant differences in the ratios of pollen grains to fungal spores on sampled areas of the insects' bodies. Data were also analyzed to determine if significant variances existed in the number of pollen grains and fungal spores on different areas of the insects' bodies: i.e., if some areas are better at carrying pollen and others better at fungal transmission. Both the raw data and the ratio of fungal spores to pollen grains were analyzed. Due to a violation of the assumption of sphericity, as indicated by Levine's test, a non-parametric Kruskal-Wallis test was performed.

Ninety pots of *R. auriculata* plants were grown from achenes collected in populations in which the fungus had not been observed to determine the rates of spread of this fungus. Achenes were scattered on the soil surface in 3.8 L black plastic nursery pots filled to within 2.5 cm of the lip with Sam's Choice® potting soil. The pots were placed in 12.7 cm deep aluminum pans filled with rainwater located at my home in Pike County, Alabama. The plants were 4 years old, and each had flowered at least twice with no evidence of the fungus being present. Plants used for each of the experiments described below were arbitrarily selected from these 90 plants.

Three experiments were undertaken during the summer of 2003. In the first experiment infected flower heads from Crenshaw County were brought back to Pike County to determine the distance the fungus could spread to uninfected plants by insect visitors or other vectors (e.g. wind, rain) in an area free of the fungus. In the first experiment, infected flower heads were supported in a single bottle of water at the same height as the inflorescences of 12 *Rudbeckia* plants. The infected heads were in the center, with the potted plants located edge to edge, and 3 pots aligned in each of the cardinal compass directions. The distance from the infection source to the centers of the pots were 9 cm, 27 cm, and 45 cm. The outside edge of the outer pots was 53 cm from the fungal source. Three replicates of this setup were arrayed for a total of 36 plants. The heads infected with the fungus were replaced with freshly collected fungus-infected heads when they began to show signs of age. The experiment continued until all potted plants were past flower.

In the second experiment, flower heads infected with fungus were again placed in a bottle of water in the center of 12 *Rudbeckia* plants, again arrayed in cardinal compass directions. This time the centers of the pots were 71 cm, 132 cm, and 254 cm from the fungus in each direction. Three replicates of this experiment were used for a total of 36 *Rudbeckia* plants. The experiment continued until all potted plants had completed flowering.

In the third experiment, uninfected potted plants were placed in the infected population in Crenshaw County to determine the distance that the fungus could spread to uninfected plants in an area with a high concentration of fungal spores available. Three pots were placed in the center of infected clumps, three along the edge of the infected population, and three pots outside of the population, 6 m from the nearest infected plant. Two replicates were used for a total of 18 pots. The experiment continued until all potted plants were past flower.

At the end of the flowering period, as determined by the withering of the ray flowers, the numbers of heads with fungus visible were counted at each distance from the fungal source. The heads were harvested and the number of individual flowers infected was counted for each distance from the source. Data were analyzed utilizing the non-parametric Spearman's correlation. All statistical analysis was performed using SPSS 11.5 for Windows with $\alpha = 0.05$.

RESULTS

Fusarium colonies were isolated from the entire length of the stems. Isolated colonies were identical to colonies isolated from infected flowers. Conidial masses on potato dextrose agar (PDA) were pale orange with aerial mycelium abundant. The reverse colony color on PDA was cream to salmon orange. Colonies grew rapidly (to 3 cm diameter after three days) and produced a fruity odor. Two types of macroconidia were observed. Macroconidia from sporodochia obtained after 10-11 days of growth on the low nutrient medium Synthetischer Nährstoffärmer Agar (SNA) were sickle-shaped, straight to slightly curved with 4-5 (rarely 6) septa equally distant (Fig. 2). The apical cell was conical, curved at the end, and penultimate. The basal cell was slightly notched. Macroconidia varied considerably, but averaged 75 µm in length and 3.7 µm in width (N = 13). Macroconidia formed from the aerial mycelium on polyphialides were straight and spindle shaped, with 2-3 septa. Microconidia formed either singularly on a monophialide or in false heads (= conidiophores) at the tips of the conidiogenous cells. Microconidia were aseptate or had 1 septum, and averaged 14.2 µm in length. They were abundantly produced in false heads, mainly from polyphialides, but also from monophialides.

Fungal spores were isolated from all 20 bees examined. Spores were found in higher ratios in those body areas (face, lower abdomen, and legs/feet) of the bee's body that come into direct contact with the flowering heads during feeding (Table 1). The Kruskal-Wallis test demonstrated a significant variance in the ratio of pollen to fungal spores for different areas of the bees' bodies. The pollen and fungal spore load varied in the same order, with pollen load being greater on all sites than fungal spore load (Table 1). Analysis of the data on the spread of the fungus on potted plants indicated a significant negative correlation between number of infections and distance from the fungal source (Tables 2, 3, 4).

DISCUSSION

In an experiment in which *Rudbeckia* heads were bagged with an insect-excluding material, significantly fewer achenes were produced than in open pollinated heads (Diamond and Boyd 2004), indicating that insects are critical for pollination of this species. However, insects transmit not only pollen but also fungal spores that could infect flowers and render them sterile.

The fitness of *R. auriculata* is reduced by infection with the plant pathogen *F. semitectum* since infected flowers fail to produce achenes. In natural populations approximately 3-5% of the plants contained at least some flower heads infected with the fungus. Infection rates within heads varied from a single flower to as much as the entire head, but were generally in the 5-10% infected range. This is less than the 20-48% infection rate for plants of *Euphorbia cyparissias*, although infection rates have been reported to vary between populations and between years (Lara and Ornelas 2003, Pfunder and Roy 2000). Other investigators have reported extremely low infection rates for plants of *Silene virginica* L. (Antonovics *et al*. 1996) and low transmission rates within long-established populations of *Silene alba* (P. Mill.) Krause (Alexander and Antonovics 1995). Low infection and transmission rates in *R. auriculata* may be due to resistant genotypes as has been demonstrated in *Silene alba* (Alexander and Antonovics 1995). As *R. auriculata* is a perennial plant that reproduces almost exclusively by the production of short stolons (Diamond and Boyd 2004), the fungus poses no serious immediate threat to local populations, and most populations remain free of infection by the fungus at this time. However, it has been suggested that disease-causing agents can affect population size, genetic variability, and community interactions of host plants (Burdon 1982). This is particularly important when dealing with a species that is already rare and restricted in distribution.

Evidence indicates that the fungus can invade the perennial parts of *Rudbeckia* plants via the stem, and that initial infection results in at least some of the plants producing diseased flower heads in subsequent years. *Fusarium* colonies were isolated from the entire length of stems that were producing infected flower heads. Three of five plants infected with the fungus in 1999 produced infected flower heads in 2000 and 2001, even though they were not re-exposed to the fungus. It is unlikely that the *Rudbeckia* infections were the result of spores released into the environment as other *Rudbeckia* plants growing in the same area, but not directly infected with the fungus, never produced visible infections. *Moussonia deppeana* (Schlechtend. et Cham.) Hanst. infected with *Fusarium moniliforma* Sheldon, and *Silene alba* infected with *Ustilago violacea* (Pers.) Roussel, both produced diseased flowers for up to four years after initial infection (Lara and Ornelas 2003, Baker 1947). *Fusarium proliferatum* (Matsushima) Nirenberg remains in the host plant and causes the recurrence of leaf spots and shoot rot for a number of years after initial infection (Uchida 2005). Thus, once a plant within a population is infected, the potential for spread to other individuals continues. That plants may remain infected for a number of years is also important in that it has been recommended that new populations of *R. auriculata* be established on protected sites within its range from achenes or plants collected from natural populations as a conservation measure for this rare species (Diamond and Boyd 2004). It would be important to select uninfected plants to establish these new populations, as infected plants would produce fewer viable achenes and thus be less effective founders.

Because insect vectors spread this pathogen, insect behavior must be considered when discussing epidemiology of the disease. It has been discovered that in many cases the fungal agents influence the behavior of insect visitors. In *Vaccinium*, the fungus *Monilinia* reflects ultraviolet light in the same range as the floral calyces and produces a sugary reward that attracts the same species that regularly serve as pollinators (Batra and Batra 1985). The insects pick up spores while feeding on the sugary solution and transmit the spores to uninfected plants or plant parts (Batra and Batra 1985). Fungal pseudo-flowers of *Arabis,* caused by the fungus *Puccinia,* share many of the same visitors that act as pollinators for *Anemone patens* L., and may influence reproductive success of that species (Roy 1996). In *Silene alba*, diseased flowers were preferred by nocturnal visitors

(Roche 1993, Real *et al.* 1992). In other cases pollinators have been shown to discriminate against flowers that are infected by fungus (Jennersten 1988b). Pfunder and Roy (2000) reported shorter visits by pollinators to fungal pseudo-flowers in *Euphorbia cyparissias*. Similar shorter visits to infected heads appear to be the case with *Fusarium* infection of *R. auriculata*. The most common insect visitor at the study site in Crenshaw County was *Andrena aliciae* (Diamond and Boyd 2004). These bees collect pollen from flowers to provision their nests, and are oligolectic on flowers of various species of Asteraceae (LaBerge 1967). In the field these insects visited infected flowers less often and spent less time on them (A. Diamond, pers. obs.). However, even though these insects appear to discriminate against fungal infected flowers, they do make mistakes as shown by field observations and the recovery of fungal spores from the bees' bodies (Table 1). This, coupled with the fact that these bees are specialists, allows the fungus to spread from flower to flower and plant to plant within the *Rudbeckia* population. These bees also tend to maximize their foraging efforts by visiting large displays of flowers and moving to the closest head on the same plant and not moving from plant to plant rapidly. This behavior of the pollinator localizes the dispersal of the fungus into a relatively small area as indicated by results of our dispersal experiments. Clumped distributions of pollinator-dispersed fungal infections and slow rates of spread of fungal pathogens have also been reported in *Silene alba* (Real *et al.* 1992) and *Silene virginica* (Antonovics *et al.* 1996).

Very little is known about fungal infections of native plants, other than a few dramatic cases such as *Silene* and members of the Brassicaceae (Cruciferae). The available literature is heavily weighted towards crop and ornamental species (Farr *et al.*

1989). This is the first report of a pathogen infecting *R. auriculata,* although this rare species has been closely monitored for over 15 years (Diamond and Boyd 2004). A *Fusarium* floral infection similar to the one reported here for *R. auriculata* was observed on plants of *Rudbeckia hirta* L. var. *pulcherrima* Farw. (*Rudbeckia bicolor* Nutt.) in Bullock County, Alabama in 2002. Microscopic examination of that fungus indicated it was slightly different from *F. semitectum* isolated from *R. auriculata*. Whether this fungus is a related species of *Fusarium* or a species-specific host race of *F. semitectum* is unknown. More research is needed to assess the distribution of this fungal pathogen and its long term effects on plant survival and reproduction.

Figure 1: *Rudbeckia auriculata* showing head with normal flowers (yellow pollen) and flowers infected with *Fusarium semitectum* (pinkish-white).

Figure 2: *Fusarium semitectum* macroconidia isolated from *R. auriculata*.

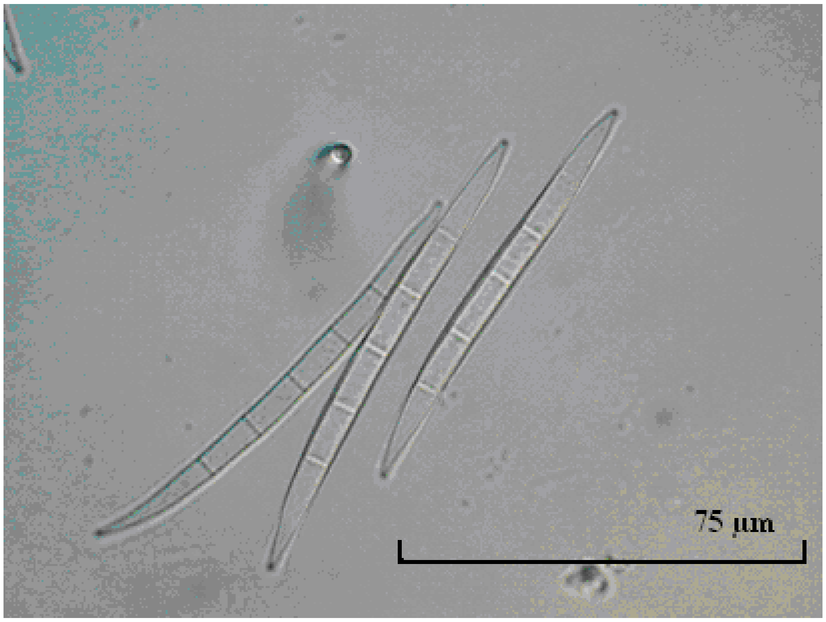

Table 1: Numbers of pollen grains and fungal spores from various locations on the bodies of *Andrena aliciae* bees collected on *Rudbeckia auriculata* plants in Crenshaw County, Alabama.

Location		Pollen grains	Fungal spores	Ratio
Lower thorax		34218	522	66:1
Upper thorax		9660	105	92:1
Lower abdomen		57678	1090	53:1
Upper abdomen		27373	445	66:1
Face		15474	347	45:1
Legs		90344	2490	36:1
Total		234747	4999	47:1

Table 2: Mean number and SD for *Rudbeckia auriculata* heads and flowers infected with *Fusarium semitectum* in pots located edge to edge. The rate of spread of the fungus indicated significant negative correlations between number of infections and the distance from the fungal source (Spearman's correlation: heads: -0.475, p = 0.003; flowers: -0.499, p = 0.002).

Distance from infection source to center of pot	Mean number of infected heads	Mean number of infected flowers
9 cm	1.83, SD = 1.01	7.74, SD = 2.58
27 cm	0.83, SD = 0.52	4.53, SD = 1.50
45 cm	0.17, SD = 0.29	1.00, SD = 1.73

Table 3: Mean number and SD for *Rudbeckia auriculata* heads and flowers infected with *Fusarium semitectum* in pots with the inside edge of the pots 61 cm, 122 cm, and 244 cm from the fungus direction. The rate of spread of the fungus indicated significant negative correlations between number of infections and the distance from the fungal source (Spearman's correlation: heads: -0.390, p = 0.019; flowers: -0.387, p = 0.020).

Distance from infection source	Mean number of infected heads	Mean number of infected flowers
61 cm	0.67, SD = 0.38	2.95, SD = 0.32
122 cm	0.17, SD = 0.29	1.00, SD = 1.73
244 cm	0	0

Table 4: Mean and SD for *Rudbeckia auriculata* heads and flowers infected with *Fusarium semitectum* on potted plants placed in the middle, at the edge, and 6 m from the nearest infected clump of *Rudbeckia auriculata* plants in Crenshaw County, Alabama. The rate of spread of the fungus indicated significant negative correlations between number of infections and the distance from the fungal source (Spearman's correlation: heads: -0.861, $p < 0.001$; flowers: -0.873, $p < 0.001$).

Location relative to infected population	Mean number of infected heads	Mean number of infected flowers
Middle	5.00, SD = 0.42	9.68, SD = 0.81
Edge	1.25, SD = 0.35	6.14, SD = 0.91
6 m	0	0

V. CONCLUSIONS

The southeastern region of the United States is an area of high biological diversity and endemism, with many species rare and vulnerable to extinction (Estill and Cruzan 2001, Ricketts *et al.* 1999, Flather *et al.* 1998, Dobson *et al.* 1997). *Rudbeckia auriculata* is one such species. Knowledge of the distribution of a species can contribute to an understanding of the possible reasons for its rarity (Fiedler 1986). The majority of *R. auriculata* populations occur in Alabama, most often in human-disturbed wetlands along roadsides and power line corridors where the plants are subject to various threats (Chapter II). The range of *R. auriculata* is disjunct with one center of populations occurring in southern Alabama and adjacent areas of Florida and Georgia, and the second center located in north-central Alabama (Chapter II). This disjuncture appears to be genuine and not an artifact of collecting. Extensive surveys resulted in the discovery of fourteen new populations including the first report for Bullock County, Alabama. Due to its large stature and ease of visibility when in flower, the discovery of substantial numbers of new populations is unlikely.

Most populations of *Rudbeckia auriculata* are small (less than 50 flowering stems). A census of flowering stems over a ten year period indicates that although the number of populations has increased slowly the number of flowering individuals has remained low. During the time span of the census five populations were extirpated and a sixth population has not been relocated since its discovery (Chapter II). Populations fluctuated in the number of flowering stems produced from year to year due to disturbance, succession, and possibly other factors such as precipitation. Succession toward hardwood forest and the lack of natural disturbance that would halt or reverse this trend appear to be a critical limiting factor for this species. Analysis of soils supporting *R. auriculata* populations indicates that nutrient concentration, pH, and soil texture are not limiting factors. Sampling of associated vegetation documented a wide range of plant species common in open wetland sites, with no species or group of species common to all sites (Chapter II).

Exclusion of visitors from inflorescences demonstrated that *Rudbeckia auriculata* is probably self-incompatible (Chapter III). Based on abundance and pollen load, the most likely pollinators are native bees: *Andrena aliciae* Robertson in medium and large populations and Halictids in small populations (Chapter III). These species demonstrate a high fidelity for *Rudbeckia* inflorescences based upon pollen samples removed from their bodies, even though other composite species were in flower at the same time (Chapter III). Insect activity is diurnal with two peaks of visitation, one in the early morning and a second in the afternoon. Smaller populations attracted fewer potential pollinators, both quantitatively and qualitatively, and as a result exhibited significantly lower achene set. Lack of pollinators, higher rates of self-pollination, and receiving pollen from closely related siblings has been demonstrated to result in lower seed set in other plant species (Oostermeijer *et al.* 1998, Pettersson 1996, Byers 1995, Johnson *et al.* 1995, Lamont *et al.* 1993, Jennersten 1988a). Achene dispersal is highly localized and dependent upon gravity, with most achenes falling within 0.3 m for the flowering stem (Chapter III).

Hydrochory may be a significant means of secondary dispersal. Recruitment experiments demonstrated that seedling establishment is poor, particularly when the soil is covered with litter, or when seedlings are in competition with other species (Chapter III).

The fungus *Fusarium semitectum* was documented infecting the flowering heads of *R. auriculata* at two sites in Alabama (Chapter IV). The fungus renders infected flowers sterile. Fungal spore masses superficially resemble pollen and are picked up by the main pollinator, *Andrena aliciae*, which likely serves as a dispersal agent for the pathogen. The fungus invades the vegetative portions of the plants, and initial infections result in at least some of the plants producing diseased flower heads in subsequent years.

The future of this species remains in doubt due to its overall rarity, the low production of viable achenes in small populations, and lack of recruitment. Additional threats include local extinctions of populations caused by roadside and power line right-of-way maintenance, invasive plant species, the draining of wetlands, and development. At this time *R. auriculata* receives no legal protection either at the federal or state level, and only two populations (both in the northern portion of the range) occur on protected sites.

However, because of the ease of propagation of *R. auriculata* from achenes, the possibility of artificially augmenting existing populations or creating new populations exists, as called for by the U. S. Fish and Wildlife Service (2003). It is recommended that new populations of this species be established on protected wetland sites within its range from achenes collected from natural populations free of the fungal pathogen *Fusarium semitectum*. Achenes should be collected in October and planted on the soil surface in open areas. Competing vegetation and leaf litter should first be removed, and the soil disturbed to promote the greatest survival of seedlings (Chapter III). Recruitment in existing populations could be aided by creating disturbed areas within 0.3 meters of existing clumps shortly before achene fall. In addition, small populations could be augmented with seedlings grown in pots and planted once they reach a sufficient size to survive competition from existing vegetation.

Further research should be undertaken on the distribution and habitat preferences of *Andrena aliciae* to determine its range and factors that may influence its abundance. In addition, the lack of existing regulatory mechanisms coupled with other threats, causes me to agree with Schotz (2000) that the U. S. Fish and Wildlife Service should re-evaluate *R. auriculata* and consider providing it some form of formal protection. These would be important first steps for the conservation of *Rudbeckia auriculata*.

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