Dionaea muscipula (Venus Flytrap) Establishment, Release, and Response of Associated Species in Mowed Patches on the Rims of Carolina Bays

James O. Luken[1,2]

Abstract

Carolina bays are depression wetlands of high conservation value that occur across the Southeastern Coastal Plain of the United States. Venus flytrap (*Dionaea muscipula*) is one rare carnivorous plant that grows in open habitats on the rims of Carolina bays. Without frequent burning, vegetation on bay rims becomes dominated by evergreen shrubs and Venus flytrap populations decline. This project examined the utility of mechanical mowing, soil clearing, transplanting, and seeding as an approach to restoring populations of Venus flytraps when fire is precluded. Mowing of patches on bay rims produced open sites with little ground-layer vegetation. After two growing seasons, adult Venus flytraps transplanted to mowed patches showed high survivorship and relatively high leaf number/plant. Suppressed Venus flytraps existing on-site quickly initiated growth in response to mowing. These volunteers and the transplants had higher flowering percentages than plants in reference populations. Seeds of Venus flytraps were scattered in mowed and cleared plots. Seedling establishment was low, but seedlings persisted into the second growing season. Mowing created suitable habitat for growth and flowering of adult Venus flytraps and facilitated establishment of two other carnivorous species, Sundew (*Drosera capillaris*) and Bladderwort (*Utricularia subulata*). But, mowing and clearing also facilitated invasion by four species of grasses and rushes; evergreen shrubs resprouted quickly after mowing. Maintaining persistent openings by mowing the rims of Carolina bays will be an ongoing challenge due to availability of potential invaders and rapid regrowth of shrubs.

Key words: carnivorous plant, Carolina bay, mowing, rare plants, Venus flytrap.

Introduction

Carolina bays are unique wetland ecosystems occurring across the Southeastern Coastal Plain of the United States. They are characterized as shallow, isolated, elliptical, depression wetlands with well-defined borders (Fig. 1). Although Carolina bays have similar shape and orientation, they are extremely variable in size, depth, soil type, and vegetation (Sharitz & Gibbons 1982; Sharitz 2003). Carolina bays were historically viewed as potential sites for agriculture and thus many show evidence of logging, tillage, or ditching (Sharitz 2003). As wetlands, Carolina bays were afforded some legal protection under the Clean Water Act, but recent court challenges to that act have greatly weakened this protection (Sharitz 2003). There is now renewed interest in understanding and restoring Carolina bays before they are irreversibly damaged (Kirkman et al. 1999).

Many Carolina bays support vegetation dominated by evergreen shrubs and thus the bays are considered as a type of shrub bog (Sharitz & Gibbons 1982). As is the case with other wetland systems (Gosz 1991), the ecotone between Carolina bays and adjacent uplands is a zone of high species richness due to mixing of populations from two distinct habitats (Kirkman et al. 1998). Furthermore, the ecotone between Carolina bays and pine savannas is an important area for plant speciation (LeBlond 2001) and for migration of various vertebrate species (Sharitz & Gibbons 1982).

In South Carolina, Carolina bays are focal points of several large nature preserves due to the guild of carnivorous plants that grow near the bays. Prescribed burning has been used in these preserves to reduce shrub stature, to direct succession, to stimulate seed germination, to remove accumulations of detritus, and to create open sites conducive to establishment and growth of herbaceous plants. This management approach is based on the understanding that the Southeastern Coastal Plain landscape was historically influenced by a high-frequency fire regimen (Wells & Whitford 1976; Gray et al. 2003) and that fire interacts with hydrology to control many aspects of plant community composition (Kirkman 1995; De Steven & Toner 2004).

In the absence of fire or management activities that mimic fire, many carnivorous plants in shrub-dominated wetlands of the southeastern United States are eliminated due to a combination of shading from shrubs and burial by litter (Brewer 1998, 1999). In the case of the Venus flytrap, development of shrub-dominated vegetation may

[1] Department of Biology, PO Box 261954, Coastal Carolina University, Conway, SC 29528, U.S.A.
[2] Address correspondence to J. O. Luken, email JoLuken@coastal.edu

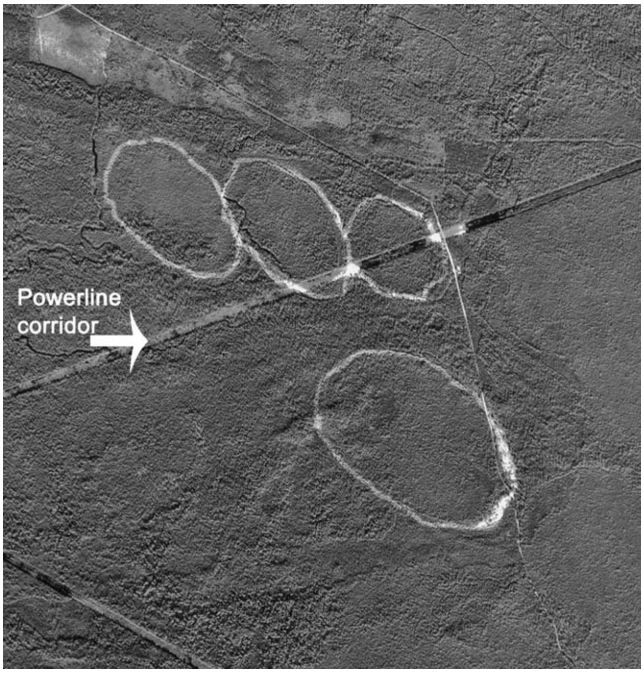

Figure 1. Carolina bays at LOBHP, South Carolina. The powerline corridor crossing two of the bays is approximately 35-m wide. Bay rims have been digitally enhanced.

also lead to reduced availability of large insects that provide nutrition necessary for plants to reach flowering size (Schulze et al. 2001). Although the Venus flytrap evolved under a high-frequency fire regimen (Roberts & Oosting 1958) and frequent prescribed burning has been identified as a critical management approach (Gray et al. 2003), the regular, planned application of prescribed fire is becoming increasingly difficult as a result of liability concerns (Yoder et al. 2004). As such, the Venus flytrap and many other endemic species associated with the Southeast Coastal Plain landscape are vulnerable to extinction (Edwards & Weakley 2001) and are now the subject of restoration efforts (Glitzenstein et al. 2001). These restoration efforts involve both plant introduction and management methods that mimic the effects of fire on community development.

This article describes the results of a project conducted at Lewis Ocean Bay Heritage Preserve (LOBHP), South Carolina, where mechanical mowing was used to create patches in Carolina bay vegetation for the establishment of new Venus flytrap populations. Carolina bays considered in this study were relatively unmodified by ditching, but the absence of frequent fire had allowed development of dense shrub-dominated vegetation on the bay rims. The following questions were addressed. What is the relative success of transplanting, seeding, and growth release of suppressed Venus flytraps as methods of increasing population sizes? How do Venus flytraps in created habitats compare to plants in reference populations? How does the plant community at the bay/savanna ecotone respond to mechanical mowing and clearing?

Methods

Focal Species

The Venus flytrap is a carnivorous plant known worldwide for its leaves modified into snap traps (Schnell 2002). Although the plant is widely distributed as a horticultural specimen, the endemic range is highly restricted. The known historical range includes the Coastal Plain of southeastern North Carolina and northeastern South Carolina (Roberts & Oosting 1958). This range roughly corresponds to the Cape Fear Arch geologic area, a hot spot of plant endemism (LeBlond 2001). The Venus flytrap typically grows at the ecotone between depression wetlands and relatively dry pine savannas although it may occur scattered throughout wet pine-dominated flatwoods (Weakley 2004). Depression wetlands associated with the Venus flytrap usually have peat accumulations, complex fire histories, and the potential for developing dense vegetation dominated by evergreen shrubs (Sharitz & Gibbons 1982). The Venus flytrap is found growing most commonly in microhabitats where past disturbances have created gaps in the shrub canopy (Luken 2005). The species is relatively rare and is assigned a G3 rank for endangerment throughout the native range.

Study Site

Restoration sites were located in LOBHP in Horry County, South Carolina (lat 33°47′N, long 78°52′W). LOBHP is a 3,640-ha tract of land that includes 22 relatively intact Carolina bays as well as extensive pine savanna. The preserve is owned and managed by the State of South Carolina. Designation of this tract of land as a Heritage Preserve was initiated in 1989. Carolina bays at LOBHP support dense, impenetrable thickets of evergreen shrubs and a tree layer comprising Pond pine (*Pinus serotina*), Swamp red bay (*Persea palustris*), and Loblolly bay (*Gordonia lasianthus*). Abandoned Loblolly pine (*Pinus taeda*) and Slash pine (*Pinus elliottii*) plantations and restored Longleaf pine (*Pinus palustris*) flatwoods surround the Carolina bays as do relatively dry sand rims supporting stunted stands of Turkey oak (*Quercus laevis*). Nomenclature of plant species follows Weakley (2004).

LOBHP is adjacent to the Grand Strand, a 30-mile section of coastal South Carolina that is a popular tourist destination. The Grand Strand is currently experiencing rapid commercial and residential development. One major road project was recently completed along the eastern edge of LOBHP; another road project is planned for the southern edge of LOBHP. These roads as well as the development of residential areas near LOBHP will greatly restrict future prescribed burning.

Rationale

Previous botanical surveys showed that viable Venus flytrap populations occurred in powerline corridors crossing through LOBHP. These populations were invariably located on the rims of Carolina bays (Fig. 1). Vegetation in powerline corridors is managed with a combination of mechanical mowing and herbicide in efforts to maintain low-growing, treeless vegetation. Presumably, historical management practices in powerline corridors at LOBHP mimicked the effects of frequent fire. However, it could not be determined if past management of vegetation in powerline corridors facilitated plant establishment or if Venus flytraps persisted from an establishment event prior to corridor construction. Carolina bay rims adjacent to the powerline corridor supported thickets of evergreen shrubs that had not been burned in recent history due to the plowing of firebreaks. These sites offered an opportunity to determine if mechanical mowing could facilitate establishment and/or release of Venus flytraps as well as other carnivorous species such as Bladderwort and Sundew.

Site Selection and Preparation

In May 2003, nine sites were chosen for restoration activities. The sites were adjacent to a powerline corridor that crossed LOBHP and were located on sloping Carolina bay rims. In May 2003, a front-mounted mechanical mower was used to remove and chop the dense shrub vegetation thereby producing nine patches. Mowed patches were 10×20 m, with the long axes running parallel to the bays (Fig. 2). Pond pines within the patches were cut and moved off-site. Two 0.5-m^2 plots were established in each patch, one at the bottom of the bay rim and the other at the top. The root mat was removed from these plots in an effort to establish a stable seedbed. These plots are hereafter referred to as mowed and cleared.

Venus Flytraps

Seeding and transplanting were tested as methods for establishing new Venus flytrap populations within the plots. In June 2003, seeds of Venus flytraps were collected from populations within LOBHP. Previous research suggested that Venus flytrap seed germination occurred within a short window of time after seed dispersal (Roberts & Oosting 1958). Therefore, the harvested seeds were immediately scattered on the soil surface of the 0.5-m^2 plots where a seedbed was established. Seeding densities were 240 seeds/plot. Adult plants were dug in June 2003 from three Venus flytrap populations at LOBHP. Three plants from each population were transplanted in 0.5-m^2 plots adjacent to the plots where seeding occurred. Planting density was equivalent to 36 plants/m^2, a density less than the mean density of 48 plants/m^2 observed in other populations (Luken 2005). Release of suppressed Venus flytraps was measured by conducting pre- and postmowing surveys in the entire patches. No plants were observed prior to mowing, however, the dense vegetation and thick accumulations of detritus may have hidden some small individuals.

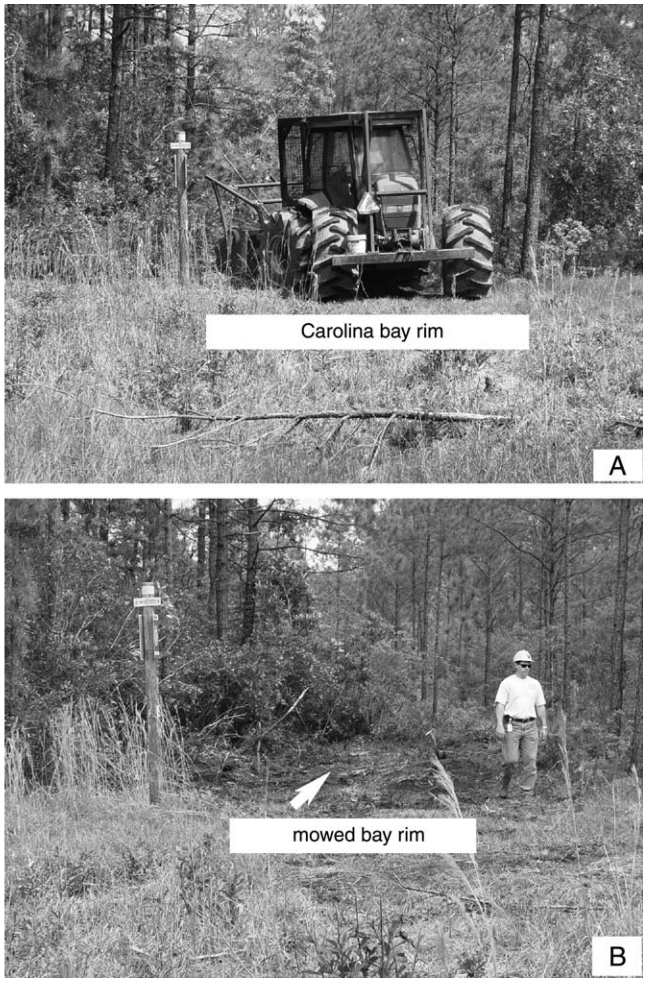

Figure 2. (A) Front-mounted mower moving into dense vegetation of a bay rim. (B) Bay rim immediately after mowing. Mowed sites were 10×20 m with the long axes running parallel to the bays.

Assessment of efforts to establish Venus flytraps occurred at the end of the first growing season and at peak flowering of the second growing season. Mowed and cleared plots were searched for established seedlings, and these were counted in September 2003 and May 2004. Survivorship of transplants was monitored, and during May of the second growing season, flowering and size of transplants were measured. Plants released from suppression within the patches, hereafter referred to as "volunteers," were counted, and a subset of these plants was also measured in May for size and flowering. Plant size was assessed with an index calculated as cumulative petiole length/plant. The size class distribution and flowering percentage of transplants and volunteers were compared to plants from two reference Venus flytrap populations occurring at LOBHP. These reference populations were in areas last burned during winter 2002 and were part of a long-term study examining Venus flytrap demography and growth. A Kruskal–Wallis one-way analysis of variance was used to determine significant differences in plant characteristics among populations. Differences in size class distributions of transplants, volunteers, and reference plants were presented as a box and whisker graph.

Plant Community Response

The response of the plant community to restoration efforts was measured in the 0.5-m^2 mowed and cleared plots where Venus flytrap seeds were introduced, in plots that were mowed but not cleared, and in plots placed in undisturbed Carolina bay vegetation. Densities of Sundew (*Drosera capillaris*) and Bladderwort (*Utricularia subulata*) were measured in early spring of 2004. These two small carnivorous plants occurred only in mowed and cleared plots and were assessed in early spring because their populations are ephemeral. Coverage of other plant species in the three categories of plots was estimated visually during July 2004. Relative cover values (total coverage of a species divided by total coverage of all species) were calculated for each plot, and communities were contrasted with nonmetric multidimensional scaling (NMDS). The NMDS was conducted with a Jaccard distance measure; starting coordinates were randomly selected, and stability of results was checked by multiple runs. Indicator Species Analysis was used to determine if particular species were associated with plots assigned to the various categories. These community analyses were done using PC-ORD (McCune & Mefford 1999). Differences in richness and diversity (H′) among the three treatments were compared with analysis of variance followed by a Tukey's test.

Results

Venus Flytraps

Only 5–7% of the Venus flytrap seeds sown in the mowed and cleared plots resulted in established seedlings (Table 1). However, seedlings persisted through the first winter, and there was evidence that further establishment occurred between the 2003 and 2004 sampling dates, at least at the bottom of bay rims where moisture was more available (Table 1). Mean survivorship of transplanted adult Venus flytraps was 85% at the bottom and 72% at the top of the bay rims, producing a mean density of 14 transplants/patch in 2004. Volunteer Venus flytraps were found in four patches producing an overall mean density of six volunteers/patch. Transplants had significantly ($p < 0.05$) higher numbers of petioles than reference plants, but maximum petiole length was not significantly different (Table 2). The percentage of plants producing flowers was highest among volunteers (93%) and lowest in the two reference populations (Table 2). The size class distributions of transplants and plants from reference populations were similar. However, the volunteer population included extremely large plants not found in reference or transplanted populations (Fig. 3).

Table 1. Mean (± SE, $n = 9$) seedling densities (no./plot) of carnivorous plants in 0.5-m^2 experimental plots (mowed and cleared) established at two topographic positions on the rims of Carolina bays in LOBHP, South Carolina.

	Position	
Species	*Bottom*	*Top*
Dionaea muscipula (2003)	12 ± 5	12 ± 4
Dionaea muscipula (2004)	18 ± 6	12 ± 4
Drosera capillaris	4 ± 2	2 ± 1
Utricularia subulata	16 ± 9	2 ± 1

Plots were positioned either at the bottom or top of the bay rims. *Dionaea muscipula* was from introduced seeds; *Drosera capillaris* and *Utricularia subulata* were from on-site seed sources.

Associated Species

Drosera capillaris and *Utricularia subulata* became established in the mowed and cleared plots during early spring of 2004 (Table 1). Later in the 2004 growing season, most of the mowed and cleared plots become dominated by grasses and rushes, whereas areas experiencing only mowing supported communities with species composition similar to undisturbed bay vegetation (Fig. 4). Undisturbed Carolina bay vegetation and mowed vegetation were dominated by the following shrubs: Large gallberry (*Ilex coriacea*), Fetterbush (*Lyonia lucida*), and Dangleberry (*Gaylussacia frondosa*). Significant ($p < 0.05$) indicators for mowed and cleared plots were *Dichanthelium erectifolium, Dichanthelium longiligulatum*, *Juncus scirpoides*, and *Rhynchospora fascicularis*. The only other significant indicator was the vine *Smilax laurifolia*, an indicator of undisturbed Carolina bay vegetation. Richness and diversity (H′) were significantly ($p < 0.05$) higher in mowed plots than in undisturbed Carolina bay vegetation (Table 3).

Discussion

Mechanical mowing is a ubiquitous method of managing ecological succession and is often used where fire is precluded (Luken 1990). Venus flytraps and carnivorous plants, in general, are adapted to relatively open, wet, nutrient-poor environments (Givnish et al. 1984), and this project demonstrated that habitats suitable for Venus flytrap growth and establishment can be temporarily created with mowing. Mowing of patches in dense shrub-dominated vegetation created relatively open environments because few ground-layer species existed prior to mowing. Light levels in the ground layer of undisturbed Carolina bay vegetation were roughly 3% of light levels measured in the mowed patches (Luken, unpublished data). Venus flytraps transplanted to mowed patches showed high survivorship; transplants and volunteers were equal to or larger than reference plants and had higher

Table 2. Characteristics of Venus flytraps when growing in various environments during summer 2004.

	Population			
	Transplants	*Volunteers*	*Reference A*	*Reference B*
Petiole number/plant	6 ± 2a	5 ± 0ab	5 ± 0b	5 ± 0b
Petiole length (mm)	19 ± 1a	24 ± 2a	22 ± 1a	22 ± 1a
Flowering percentage	63	93	20	21

Transplants were moved to mowed plots during summer 2003. Volunteers emerged from suppression in mowed plots. Reference populations were last burned in winter 2002. Data for petiole number/plant and maximum petiole length (mm) are means ± SE with n = 125, 30, and 66 and 69 for transplants, volunteers, and reference plants, respectively. Means with different letters are significantly ($p < 0.05$) different.

flowering percentages. The results suggest two aspects of Venus flytrap biology. First, it is clear that suppressed Venus flytrap plants do persist in the soils of dense stands of shrubs. These plants have the ability to quickly initiate growth in response to increased light availability, a trait likely of value in shrub-dominated vegetation that is fast growing and frequently burned. Second, Venus flytraps can be readily transplanted to new habitats. This and the fact that Venus flytraps have been successfully introduced far outside the native range (Smith 1972) suggests that suitable habitat may be widespread, provided barriers to dispersal and establishment are overcome (Roberts & Oosting 1958). Glitzenstein et al. (2001) reached a similar conclusion regarding many rare species characteristic of longleaf pine communities in the southeastern United States. Results of the research at LOBHP suggest that Venus flytrap seedling establishment is a low-probability event, one that is likely dependent on availability of soil microhabitats as well as the maintenance of high light levels (Luken 2005).

Although one mowing event on the rims of Carolina bays may indeed create a short-term environment suitable for growth of transplants and release of suppressed Venus flytraps, future viability of Venus flytraps depends on how the plant community responds to mowing. When mowing was done in combination with clearing, *Drosera capillaris* and *Utricularia subulata* became established. Similar responses were noted in Mississippi wet pine savannas with the conclusion that these annual carnivorous species function as a unique class of fugitives adapted to low-nutrient environments (Brewer 1998, 1999). Because of

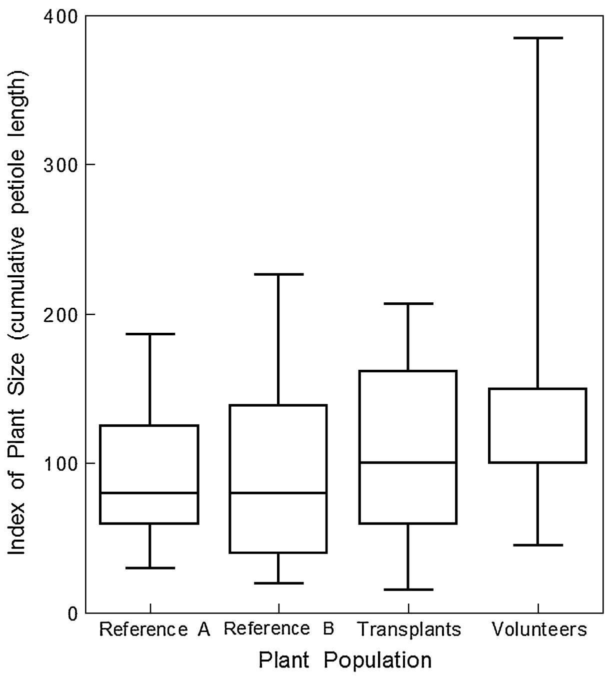

Figure 3. Box and whisker graph showing size class distributions of Venus flytrap transplants ($n = 125$), volunteers ($n = 30$), and plants from two reference populations ($n = 66$ and 69).

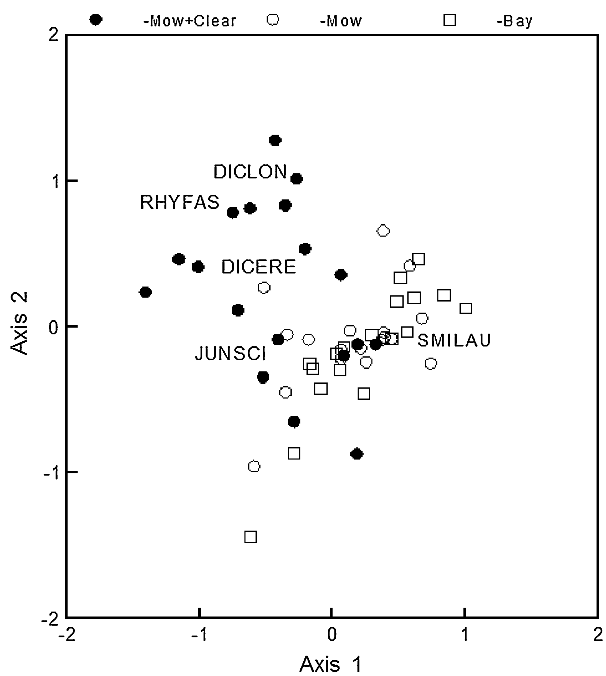

Figure 4. Ordination NMDS of communities and species in mowed and cleared plots (Mow + Clear), in mowed plots (Mow), and in undisturbed bay vegetation (Bay). Only significant ($p < 0.05$) indicator species are shown on the ordination. Species abbreviations are as follows: DICERE = *Dichanthelium erectifolium*, DICLON = *Dichanthelium longiligulatum*, JUNSCI = *Juncus scirpoides*, RHYFAS = *Rhynchospora fascicularis*, and SMILAU = *Smilax laurifolia*.

Table 3. Diversity (H′) and richness (no. of species/plot) of ground-layer vegetation on the rims of Carolina bays.

	Treatment		
	M + C	*M*	*B*
Richness	5.4 ± 0.4a	4.7 ± 0.3a	2.9 ± 0.2b
Diversity	1.2 ± 0.1a	1.1 ± 0.1a	0.8 ± 0.1b

Means (±SE, $n = 18$) are presented for plots that were mowed and cleared (M + C), for plots that were mowed (M), and for undisturbed Carolina bay vegetation (B). Means with different letters are significantly ($p < 0.05$) different.

small stature, these plants will not compete with Venus flytraps and should be considered an ancillary benefit of managing for the focal species. However, mowed and cleared plots were also quickly invaded by grasses, rushes, and sedges. Kirkman & Sharitz (1994) found that perennial grasses invaded and dominated Carolina bay vegetation when soils were disturbed by tillage. They concluded that repeated disturbance will be required to ensure establishment and growth of relatively rare species (Kirkman & Sharitz 1994). Alternatively, in areas that were mowed but not cleared, shrubs resprouted and reestablished the shrub-dominated community of the bay rim. Such shrub thickets are also a long-term problem for maintenance of plant diversity (Wilkins et al. 1993; Brewer 2002).

The present study as well as others (Kirkman & Sharitz 1994; Kirkman 1995; Poiani & Dixon 1995; Kirkman et al. 1998) suggest that the ground-layer vegetation of Carolina bay interior and edge communities may be dominated by monocots or shrubs depending on disturbance type and hydrology. In the absence of disturbance, dense shrub thickets emerge and diversity declines. Due to the tendency of Carolina bays to support tall, dense vegetation, maintaining persistent openings will be a challenge for resource managers. Furthermore, long-term viability of Venus flytraps in large nature preserves depends on maintaining metapopulations scattered along the Carolina bay rims, a requirement that will invoke some understanding of how Venus flytraps respond to the size and isolation of openings in the shrub-dominated vegetation (Quintana-Ascencio & Menges 1996). Previous research at LOBHP documented that *Sphagnum* mosses are good indicators of Venus flytrap habitat and that these same *Sphagnum*-dominated sites also support relatively less vascular plant coverage (Luken 2005). Because it is not economically feasible to repeatedly mow large natural areas (Luken 1990), future research will focus on these relatively stable *Sphagnum* openings as sites for Venus flytrap introduction and management of shrub vegetation while not allowing invasion by monocots.

Acknowledgments

This project was supported by the National Fish and Wildlife Foundation, South Carolina Department of Natural Resources, Santee Cooper Power, and Coastal Carolina University. Jamie Dozier and Ken Sott facilitated the field operations. Scott Ryder and Hugh Biggs helped with monitoring. John Thieret provided his taxonomic expertise.

LITERATURE CITED

Brewer, J. S. 1998. Effects of competition and litter on a carnivorous plant, *Drosera capillaris* (Droseraceae). American Journal of Botany **85:**1592–1596.

Brewer, J. S. 1999. Effects of competition, litter, and disturbance on an annual carnivorous plant (*Utricularia juncea*). Plant Ecology **140:**159–165.

Brewer, J. S. 2002. Disturbances increase seedling emergence of an invasive shrub in pitcher-plant bogs. Natural Areas Journal **22:**4–10.

De Steven, D., and M. M. Toner. 2004. Vegetation of upper coastal plain depression wetlands: environmental templates and wetland dynamics within a landscape framework. Wetlands **24:**23–42.

Edwards, A. E., and A. S. Weakley. 2001. Population biology and management of rare plants in depression wetlands of the southeastern Coastal Plain. Natural Areas Journal **21:**12–35.

Givnish, T. J., E. L. Burkhardt, R. E. Happel, and J. D. Weintraub. 1984. Carnivory in the bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist, nutrient-poor habitats. American Naturalist **124:**479–497.

Glitzenstein, J. S., D. R. Streng, D. D. Wade, and J. Brubaker. 2001. Starting new populations of longleaf pine ground-layer plants in the outer coastal plain of South Carolina, USA. Natural Areas Journal **21:**89–110.

Gosz, J. R. 1991. Fundamental ecological characteristics of landscape boundaries. Pages 8–30 in M. M. Holland, P. G. Risser, and R. J. Naiman, editors. Ecotones, the role of landscape boundaries in the management and restoration of changing environments. Chapman and Hall, New York.

Gray, J. B., T. R. Wentworth, and C. Brownie. 2003. Extinction, colonization, and persistence of rare vascular flora in the longleaf pine-wiregrass ecosystem: responses to fire frequency and population size. Natural Areas Journal **23:**210–219.

Kirkman, L. K. 1995. Impacts of fire and hydrological regimes on vegetation in depression wetlands of the southeastern USA. Pages 10–20 in S. I. Cerulean and R. T. Engstrom, editors. Fire in wetlands: a management perspective. Proceedings of the Tall Timbers Fire Ecology Conference, No. 19. Tall Timbers Research Station, Tallahassee, Florida.

Kirkman, L. K., M. B. Drew, L. T. West, and E. R. Blood. 1998. Ecotone characterization between upland longleaf pine/wiregrass stands and seasonally-ponded isolated wetlands. Wetlands **18:**346–364.

Kirkman, L. K., S. W. Golladay, L. Laclaire, and R. Sutter. 1999. Biodiversity in southeastern, seasonally ponded, isolated wetlands: management and policy perspectives for research and conservation. Journal of the North American Benthological Society **18:**553–562.

Kirkman, L. K., and R. R. Sharitz. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina bays in South Carolina. Ecological Applications **4:**177–188.

LeBlond, R. J. 2001. Endemic plants of the Cape Fear Arch region. Castanea **66:**83–97.

Luken, J. O. 1990. Directing ecological succession. Chapman and Hall, London, United Kingdom.

Luken, J. O. 2005. Habitats of the Venus' fly trap (*Dionaea muscipula*), Droseraceae, associated with Carolina bays. Southeastern Naturalist (in press).

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, Version 4. MjM Software Design, Gleneden Beach, Oregon.

Poiani, K. A., and P. M. Dixon. 1995. Seed banks of Carolina bays: potential contributions from surrounding landscape vegetation. American Midland Naturalist **134:**140–154.

Quintana-Ascencio, P. F., and E. S. Menges. 1996. Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. Conservation Biology **10:**1210–1219.

Roberts, P. R., and H. J. Oosting. 1958. Responses of venus fly trap (*Dionaea muscipula*) to factors involved in its endemism. Ecological Monographs **28:**193–218.

Schnell, D. E. 2002. Carnivorous plants of the United States and Canada. Timber Press, Portland, Oregon.

Schulze, W., E. D. Schulze, I. Schulze, and R. Oren. 2001. Quantification of insect nitrogen utilization by the venus fly trap *Dionaea muscipula* catching prey with highly variable isotope signatures. Journal of Experimental Botany **52:**1041–1049.

Sharitz, R. R. 2003. Carolina bay wetlands: unique habitats of the southeastern United States. Wetlands **23:**550–562.

Sharitz, R. R., and J. W. Gibbons. 1982. The ecology of southeastern shrub bogs (pocosins) and Carolina bays: a community profile. U.S. Fish and Wildlife Service, Division of Biological Services, Washington D.C.

Smith, A. P. 1972. Survival and seed production of transplants of *Dionaea muscipula* in the New Jersey Pine Barrens. Bulletin of the Torrey Botanical Club **99:**145–146.

Weakley, A. B. 2004. Flora of the Carolinas and Virginia. Working draft. University of North Carolina, Chapel Hill (available from http://www.herbarium.unc.edu) accessed on 31 August 2004.

Wells, B. W., and L. A. Whitford. 1976. History of stream head swamp forests, pocosins and savannas in the southeast. The Journal of the Elisha Mitchell Science Society **92:**148–150.

Wilkins, R. W., W. R. Marion, D. G. Neary, and G. W. Tanner. 1993. Vascular plant dynamics following hexazinone site preparation in the lower Coastal Plain. Canadian Journal of Forest Research **23:**2216–2229.

Yoder, J., D. Engle, and S. Fuhlendorf. 2004. Liability, incentives, and prescribed fire for ecosystem management. Frontiers in Ecology and the Environment **2:**361–366.