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Performance of *Dionaea muscipula* as influenced by developing vegetation¹

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LUKEN, J. O. (Department of Biology, Coastal Carolina University, Conway, SC 29528). Performance of *Dionaea muscipula* as influenced by developing vegetation. J. Torrey Bot. Soc. 134: 45–52. 2007.—Demography, growth, and flowering of *Dionaea muscipula* (Venus' fly trap) were studied during three years (2003–2005) following prescribed fire. Data were collected in permanent quadrats where the developing vegetation was either repeatedly clipped or allowed to grow. Clipping increased light availability at the soil surface. Over the study period, seedling establishment and flowering declined with increasing time since the last prescribed burn. Seedling densities did not differ between clipped and control quadrats, although greater numbers of seedlings grew to adult size in control quadrats and this significantly influenced population size-class structure. Clipping had no effect on leaf number or senescence, but plants in control plots were larger and had marginally longer petioles. The plant populations initially mapped in 2003 showed a continuous decline throughout the study and this decline was punctuated by temporary senescence linked to drought conditions. Drought-induced senescence had a persistent influence on plant size. Relatively higher seedling recruitment to the adult population in control quadrats produced an overall population increase of 18% as compared to a 17% decline in the population from clipped quadrats. *Dionaea muscipula* may have limited ability to respond to increased light availability due to leaf development constraints and repeated drought-induced senescence. Fire-dependence may best be defined in terms of seedling establishment and stimulation of flowering. Consistent soil moisture is critical to *Dionaea muscipula* but the species has characteristics that allow persistence across a wide range of vegetation trajectories.

Key words: carnivorous plant, clipping, demography, *Dionaea muscipula*, fire-dependence, seedling establishment, Venus' fly trap.

The southeastern United States is generally recognized as a region of high plant endemism (Estill and Cruzan 2001) and among these endemic plants are many relatively rare fire-dependent perennial herbs (Walker 1993, Glitzenstein et al. 2001, LeBlond 2001). While numerous studies have documented changes in presence/absence or importance of these species under varying fire regimens, far fewer studies have focused on long-term demography in an effort to determine how fire—or lack thereof—interacts with specific life history stages (Menges and Kimmich 1996, Kirkman et al. 1998, Brewer 2001, Lacey et al. 2001, Walker and Silletti 2005). Such demographic

data, however, are necessary to develop management protocols ensuring long-term population viability (Schemske et al. 1994).

Carnivorous perennial herbs of the southeast tend to occur in or near wetlands where nutrient availability is limited and where succession can lead to dense woody vegetation (Folkerts 1982, Schnell 2002, Brewer 2005). Fire-dependence among these species is theoretically explained in terms of allocation shifts in response to vegetation development and the corresponding low light conditions. These shifts decrease the plant's abilities to capture prey but increase the plant's abilities to absorb light (Givnish et al. 1984). Frequent fires maintain low or open vegetation where fitness of carnivorous species is maximized (Givnish et al. 1984). Brewer (2005) hypothesized that *Sarracenia* species should respond to increased light availability by greater allocation to prey capture vis-à-vis photosynthetic tissue. However, this hypothesis, as tested by removal of neighboring plants from *Sarracenia rubra* Walt. spp. *alabamensis* (Case and Case) Schnell and *Sarracenia alata* (Wood) Wood, was not universally accepted (Brewer 1999, 2005) even though a previous study indicated that fire increased foliage production of *Sarracenia* species (Barker and Williamson

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1988). Many questions remain regarding how physiological and demographic parameters of carnivorous species respond to surrounding vegetation (Zamora et al. 1998, Brewer 2005).

Dionaea muscipula Ellis (Droseraceae, Venus' fly trap) is a monotypic carnivorous species endemic to the Carolinas (Roberts and Oosting 1958). The snap trap of *D. muscipula* is a modified leaf blade and the winged petiole subtending the trap is modified for photosynthetic activity. Roberts and Oosting (1958) found that *D. muscipula* produces relatively long, thin petioles during summer and relatively short, wide petioles during winter. Givnish et al. (1984) interpreted this observation in support of decreased allocation to prey capture when light is limiting. Furthermore, Schulze et al. (2001) proposed that increased height and density of competing vegetation during fire-free periods leads to both light limitation and prey limitation for *D. muscipula*.

Although an overwhelming number of studies conclude that *Dionaea muscipula* will show local extinction in the absence of fire due to light, insect and nitrogen limitation (Roberts and Oosting 1958, Schulze et al. 2001, Gray et al. 2003), no studies to date have carefully monitored plant demography during a fire-free period. Unlike some species of *Sarracenia* (Ellison and Gotelli 2002), *D. muscipula* has little or no flexibility in producing leaves not structured for prey capture (Smith 1931). There is evidence suggesting that *D. muscipula* can persist in a dormant state during fire-free periods and then quickly initiate growth when tall shrub vegetation is removed (Luken 2005a) and the species also occurs in open habitats where fire is not a common disturbance (Roberts and Oosting 1958, Luken 2005b). This paper presents demographic data on *D. muscipula* in the context of a field experiment where surrounding vegetation was either clipped or allowed to grow following a prescribed fire. These questions were addressed: Does removal of surrounding vegetation affect the establishment, growth and survival of *D. muscipula*? Does *D. muscipula* change allocation patterns in response to shading by tall vegetation? And finally, what habitat factors are critical to the performance of *D. muscipula*?

Materials and Methods. STUDY SITE. *Dionaea muscipula* populations in this project

occurred at Lewis Ocean Bay Heritage Preserve (LOBHP) in Horry County, South Carolina (lat 33°47'N, long 78°52'W). Lewis Ocean Bay Heritage Preserve includes 3640 ha of protected land and 22 relatively undisturbed Carolina bays. The preserve is owned by the State of South Carolina and is managed by regulated land use and prescribed burning. The field experiment presented here focused on an area located between a Carolina bay wetland and a pine flatwoods community. In this ecotonal area, the vegetation was dominated by evergreen shrubs and vines last burned during late winter, 2002.

FIELD EXPERIMENT. *Dionaea muscipula* plants were located during 2002 by conducting a broad reconnaissance of the study area. When plants were located, a 0.25 m² quadrat was positioned over the plants and the quadrat corners were permanently staked. Then, a second group of plants was located and staked in the same general area. This process eventually provided 10 pairs of quadrats. One quadrat from each pair was randomly chosen for repeated ground-level clipping of all vascular plants except *D. muscipula* and one quadrat served as a control. Prior to clipping, each quadrat was assessed in terms of plant coverage during spring, 2003. Then, quadrats assigned to the clip treatment were clipped repeatedly over three growing seasons and the mean \pm SE cumulative oven-dry (70°C) mass of clipped vegetation was 315 \pm 41 g m⁻². *Dionaea muscipula* density ranged from 4 to 96 plants per m² (mean density, plants per m² \pm SE was 41.6 \pm 6.1 for clipped quadrats and 46.4 \pm 9.9 for control quadrats). There was no significant difference (*t*-test, *n* = 10, *P* = 0.686) in initial plant density. There were 220 adult plants mapped at the beginning of the monitoring period with 116 in control quadrats and 104 in clipped quadrats. Associated vascular plant species with the five highest frequencies were *Vaccinium crassifolium* Andrews (80%), *Ilex coriacea* (Pursh) Chapman (70%), *Clethra alnifolia* L. (65%), *Lyonia lucida* (Lam.) K. Koch (50%), and *Osmunda cinnamomea* L. (45%). Associated nonvascular plant species were *Sphagnum molle* Sull. and *Sphagnum tenerum* Sull. & Lesq. with frequencies of 50% and 40%, respectively.

Measurements of photosynthetically active radiation (PAR) were taken with a Licor LI-250A prior to clipping and after clipping was

initiated in August, 2003. In each quadrat the sensor was positioned on five points at ground level. Light measurements were expressed as a percentage of full sun as measured above the shrub layer. Prior to clipping there was no significant difference (t -test, $n = 10$, $P = 0.234$) in light availability between quadrats assigned to control and clip treatments. However, after clipping was initiated there was a significant difference (t -test, $n = 10$, $P < 0.001$). In control plots, light availability at ground level was on average 27% of full sun while light availability in clipped plots was on average 87% of full sun.

PLANT MEASUREMENTS. All *Dionaea muscipula* plants growing in the quadrats were mapped and assigned to a size class at the time of initial clipping in June, 2003. Plants mapped at this time are hereafter referred to as plants in the initial sample. Size classes of established plants were based on maximum petiole length in increments of 1 cm. Seedlings were identified by the presence of embryonic leaves and were considered a separate size class. It was not possible to assess true mortality as *D. muscipula* plants can show complete above ground senescence followed by regrowth. However, senescence was a response of interest and thus senescence was assessed as the absence of active, above-ground plant parts. Monitoring of the mapped plants occurred in spring and fall of 2003, in spring and fall of 2004 and in spring of 2005.

A subset of the initially mapped plants (2 to 4 per quadrat, $n = 59$ plants) was selected for more extensive measurements of size. These plants were measured in terms of number of leaves (petiole + trap) and lengths of petioles. An index of plant size was calculated as total petiole length per plant.

DATA ANALYSES. Data were analyzed primarily to assess the effects of the experimental treatment (clipping) on plant performance over the entire monitoring period. The monitoring period included four sample dates: August 2003, May 2004, September 2004, and June 2000. New seedlings were observed primarily in August 2003 and in May 2004. Repeated measures ANOVA on square root transformed data was performed for various plant characteristics summarized at the quadrat level. Seedling establishment was indexed in two ways: the number of newly established

seedlings per m^2 and the total number of seedlings per m^2 . Seedlings observed on the first two monitoring dates either senesced or made the transition to adult size classes. As such, recruitment of new plants into the quadrats was indexed as the number of active (with visible leaves) new plants per m^2 relative to the number of active plants per m^2 mapped in the initial sample. Activity of plants mapped in the initial sample was indexed by counting the number of these plants per m^2 with leaves. Leaf display was indexed as the number of leaves per m^2 relative to the number of leaves per m^2 in the initial sample. Petiole display was indexed as the cumulative petiole length per m^2 relative to the cumulative petiole length per m^2 in the initial sample. Senescence was indexed as the cumulative number of plants (seedlings and adults) senesced relative to the number of potentially active plants (seedlings and adults).

A population level assessment was conducted by combining size-class data for plants in the quadrats. Differences in size-class distributions between the two populations (plants in clipped quadrats and plants in control quadrats) on the initial sample date and the final sample date were assessed by performing separate Mann-Whitney tests on the ordinal data. The association between size-class and flowering was assessed with 2×3 crosstabulations (2 flowering categories and 3 size categories) and Pearson Chi-Square as the test statistic. Due to lack of widespread flowering, this analysis was done by looking only at the association between size-class in August 2003 and flowering in May 2004. All statistical analyses were done using SPSS version 11.5 (SPSS 2002).

Results. SEEDLINGS. Seedling establishment was highest in 2003 and declined throughout the study period (Fig. 1). Seedling establishment was highly variable from quadrat to quadrat ranging from 0–160 seedlings per m^2 . There were no significant ($P = 0.473$ and 0.302) effects of clipping on density of new seedlings or on total density of seedlings (Table 1). However, a significantly higher percentage (t -test for quadrats with seedlings on the final date, $P = 0.047$) of seedlings establishing in clipped quadrats had senesced by the end of the monitoring period (mean \pm SE, $94 \pm 5\%$ vs. $59 \pm 13\%$ in control quadrats). This higher senescence in clipped quadrats was indexed as a marginally significant ($P = 0.034$) effect of

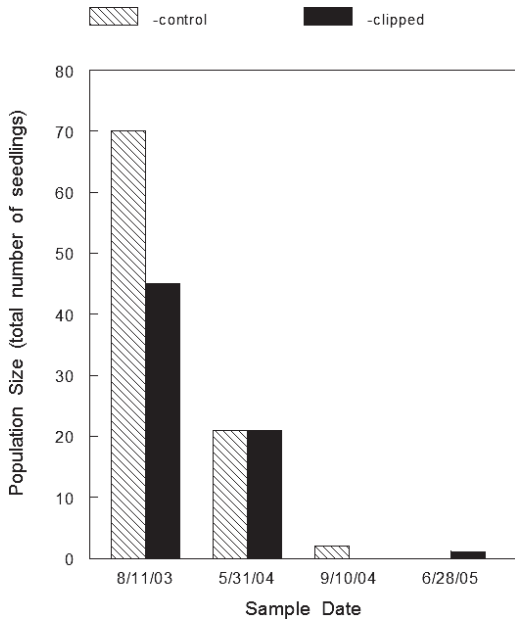


FIG. 1. Total numbers of new *Dionaea muscipula* seedlings mapped in clipped or control quadrats on various sample dates. The study area was last burned in 2002.

clipping on overall recruitment of new, active plants into the quadrats (Table 1). Recruitment was generally lower in clipped quadrats where mean recruitment indices ranged from 0.2–1.3 vs. 0.4–2.1 in control quadrats.

ADULT PLANTS. In control and clipped quadrats there was constant loss of plants

due to senescence (Fig. 2a). This trend in plant loss was punctuated by temporary senescence during a prolonged drought in spring, 2004 when plants withered and then resumed growth in fall (Fig 2b). After spring, 2004, recovery of plant size continued to the final sample date (Fig. 2b). There was no significant ($P = 0.565$) effect of clipping on active plant density (Table 1) and no significant ($P = 0.508$) effect of clipping on the index of senescence. However, the size index for plants in control quadrats (Fig. 2b) was consistently higher ($F_{1,18} = 3.65$, $P = 0.072$). The size index was influenced by both leaf number and petiole length. Table (1) shows that clipping had no significant ($P = 0.121$) effect on leaf display although it did have a marginally significant ($P = 0.038$) effect on petiole display. Mean petiole display indices ranged from 0.36–0.91 in clipped plots vs. 0.52–1.05 in control plots.

POPULATION-LEVEL CHARACTERISTICS. Over the study period the population in control quadrats increased from 116 to 137 plants, a change of 18%. In contrast, the population in clipped plots decreased from 104 to 86 plants, a decline of 17%. Initially, plant size-class distributions in control and clipped quadrats were marginally different ($P = 0.041$) due to greater numbers of class 2 plants and lower numbers of class 4 plants in control quadrats (Fig. 3). At the end of the monitoring period the difference between size-class distributions was greater ($P < 0.001$) due to

Table 1. Summary of repeated measures ANOVA results for various characteristics of *Dionaea muscipula* plants growing in experimental quadrats. Data were square root transformed and statistical results are for the between subjects effect of clipping. Typically, there were four sample dates except in the case of seedlings where only two sample dates were included. Response shows the untransformed mean value \pm SE of the characteristic on the final included sample date for clipped quadrats (CL) and controls (CO), $n = 10$.

Characteristics	$F_{1,18}$	P	Response	
			CL	CO
New seedlings (# per m ²)	0.538	0.473	9.6 \pm 5.2	9.6 \pm 5.6
Total seedlings (# per m ²)	1.127	0.302	25.2 \pm 15.6	29.6 \pm 6.8
Recruitment ^a	5.272	0.034	0.02 \pm 0.01	0.39 \pm 0.16
Active plant density ^b	0.205	0.565	37.6 \pm 5.6	40.0 \pm 8.4
Leaf display ^c	2.656	0.121	0.73 \pm 0.45	0.97 \pm 0.14
Petiole display ^d	5.044	0.038	0.91 \pm 0.15	1.18 \pm 0.21
Senescence ^e	0.456	0.508	0.35 \pm 0.09	0.41 \pm 0.09

^a Number of active new plants established per m² relative to the number of active plants per m² from the initial sample.

^b Number of active plants from the initial sample per m².

^c Number of leaves per m² relative to the number of leaves per m² in the initial sample.

^d Cumulative petiole length per m² relative to the cumulative petiole length per m² in the initial sample.

^e Number of plants senesced per m² (seedlings + adults) relative to the total number of potentially active plants per m² (seedlings + adults).

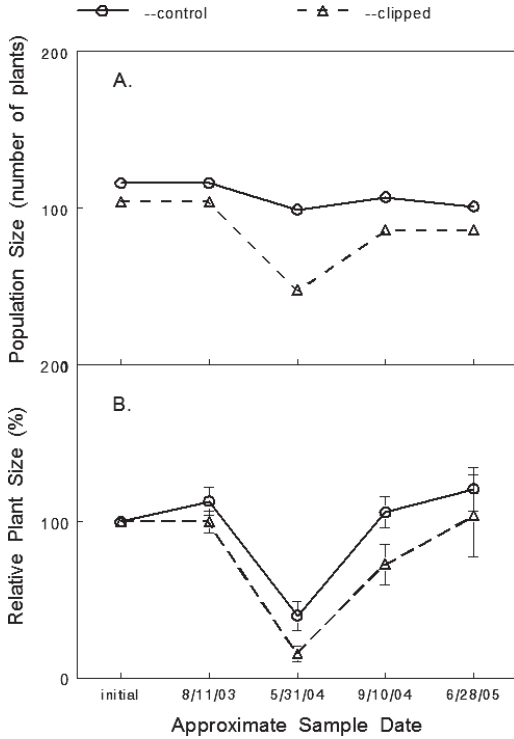


FIG. 2. A. Population trends of active, adult *Dionaea muscipula* plants mapped at the beginning of a field experiment and followed from spring, 2003 to spring, 2005. Points on the line represent the total number of plants from clipped or control quadrats. B. Mean relative size index of *Dionaea muscipula* plants growing in clipped or control quadrats. The size index was calculated as total petiole length per m² expressed relative to total petiole length per m² at the beginning of the monitoring period. Means \pm SE, $n = 10$.

higher recruitment of small plants in control quadrats (Fig. 3). Higher petiole lengths of plants growing in control plots (Table 1) did not lead to an overall shift toward larger size classes (Fig. 3). In 2003, flowering percentages were 55% and 58% for plants growing in clipped and control plots, respectively. These percentages dropped to 21 and 28% in 2004 and to 7% for both treatment groups in 2005. Plant size and flowering were significantly associated in plant populations from both experimental treatments (Pearson Chi-Square, $P = 0.022$ in control quadrats and $P = 0.011$ in clipped quadrats) with higher flowering percentages in the larger size classes.

Discussion. If fire dependence in *Dionaea muscipula* is associated with the inability of plants to thrive in low light environments, then

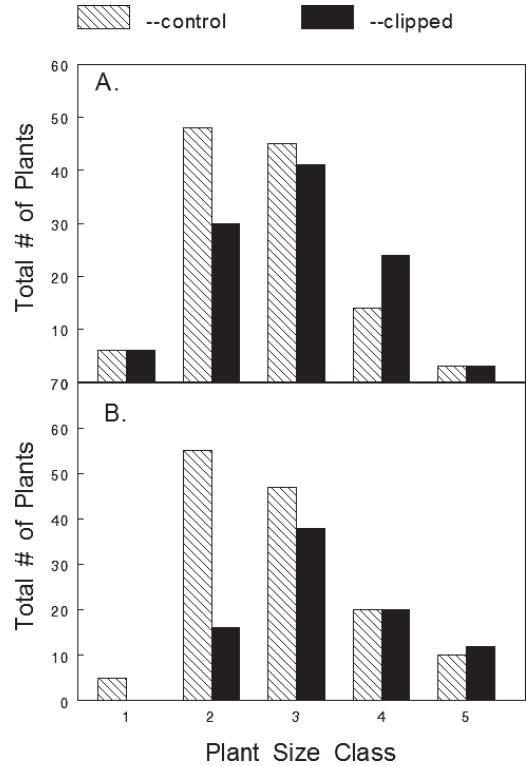


FIG. 3. A. Size-class structures of *Dionaea muscipula* plants growing in clipped and control quadrats on the initial sample date of the field experiment. Plants were placed in size classes based on maximum petiole length. $n = 116$ and $n = 104$ for control and clipped quadrats, respectively. B. Size-class structures on the final date of the field experiment. $n = 137$ and $n = 86$ for control and clipped quadrats, respectively.

this study should have demonstrated one or all of the following trends in control quadrats: higher senescence rates, lower growth rates, lower flowering percentages and lower seedling establishment. Furthermore, if competing vegetation is the major determinant of plant size, trap size and insect capture (Schulze et al. 2001), then plants in clipped plots should have grown relatively larger. And finally, if carnivorous plants achieve greatest fitness in high light environments, then plants in clipped plots should have responded by producing more leaves with longer petioles (Givnish et al. 1984). This relatively short field experiment (three growing seasons) did not support any of these expectations. Instead, plants in control quadrats that experienced lower light levels produced longer petioles and recruitment of new plants into these quadrats was higher. The

results can be interpreted with the understanding that clipping modifies primarily the light environment while fire may have more complex environmental impacts.

Dionaea muscipula is difficult to study in the field. It is a small, relatively rare, cryptic plant species where the leaf is highly modified and relative change in leaf parameters occurs within multiple episodes of leaf senescence followed by regrowth. At best, this study was able to track numbers of leaves and lengths of petioles in a small sample. However, due to plant size and growth habit, it was not possible to assess leaf production and turnover without severely disrupting plants and the surrounding microhabitat. Accurate measurement of leaf and root production is essential to understanding whole plant growth and allocation shift. Even death in *D. muscipula* is difficult to assess simply from presence or absence of above ground structures due to the potential of plants to persist belowground for an unknown period of time in a dormant state (Luken 2005a). Finally, this experiment was conducted in a single type of shrub-dominated vegetation where *D. muscipula* occurred in small metapopulations and because the clipped quadrats were relatively small, the results should be interpreted and applied with caution.

Luken (2005a) demonstrated that clearing of dense vegetation stimulated flowering of suppressed plants and facilitated seedling establishment. Similarly, the current study demonstrated highest flowering and seedling establishment soon after prescribed fire. Although high light associated with canopy opening appears to stimulate flowering in *Dionaea muscipula*, such conditions do not lead to higher seedling survivorship likely as a result of increased desiccation risk. Only rarely did seedlings recover from a senescence event and when seedlings senesced, no above-ground plant parts were visible. Standing vegetation in control plants may have provided some degree of protection allowing higher seedling survival. Conversely, clipping may have increased evaporation from the soil surface and thus accelerated seedling mortality. Previous research demonstrated that *D. muscipula* seedlings were overrepresented in wet, bare microhabitats while adult plants were overrepresented on *Sphagnum* mosses leading to the tentative hypothesis that moisture conditions in *Sphagnum* mosses are

conducive to long-term survival and growth of *D. muscipula* (Luken 2005b).

The decline in adult population size noted for spring, 2004, was due to drought. In contrast to seedlings, one could locate the blackened and withered leaves of senesced adults and most of these plants resumed growth when moisture conditions improved. However, full recovery of plant size was not complete months later. In *Dionaea muscipula*, drought-induced senescence may be particularly detrimental as both light and insect capture are halted until new leaves are produced. The pattern of population change in *D. muscipula* was similar to that observed for the endangered orchid *Isotria medeoloides* (Pursh) Raf., where populations are also comprised of active and temporarily senescent individuals (Mehrhoff 1989).

It is difficult to categorize *Dionaea muscipula* solely as a low- or high-resource species (sensu Chapin et al. 1993). Considering only leaf display, one might conclude that it is a low-resource species and is thus unable to quickly change growth or allocation in response to increased resource availability. *Dionaea muscipula* did show some plasticity of leaf (petiole) length. Petioles in control quadrats were longer but the response was small and the effect on plant performance was not clear. Conversely, allocation theory regarding carnivorous species (Givnish et al. 1984) predicts that low light conditions in the control quadrats should lead to shorter petioles. Relatively longer petioles of plants in control quadrats may be a response to developing vegetation and shade rather than a response to high light (Roberts and Oosting 1958) as was observed for the terrestrial orchid *Dactylorhiza majalis* (Rchb.) P.F. Hunt & Summerh. under different mowing regimens (Janeckova et al. 2006). Options for leaf allocation change are likely limited due the following constraints. Trap length and petiole length are correlated ($r = 0.71$) and essentially all leaves produce traps throughout all leaf development stages (Smith 1931, Roberts and Oosting 1958). In order for plants to increase trap size and thus catch larger insects (Gibson 1991, Schulze et al. 2001), the petiole must also increase in length but such extension of the petiole may entail decreased photosynthetic surface (Roberts and Oosting 1958, Givnish et al. 1984). Classification of *D. muscipula* as a low-resource species is also supported by its

high nutrient use efficiency (Adamec 2002). In contrast to relatively limited leaf plasticity, *D. muscipula* can respond relatively quickly to disturbance by flowering and by rapid re-growth (Luken 2005a). These traits are more characteristic of high-resource species (sensu Chapin et al. 1993) and are related to plant size, energy storage in below-ground structures as well as disturbance history (Mehrhoff 1989, Luken 2005a, Walker and Silletti 2005). Brewer (2005) found that *Sarracenia rubra* spp. *alabamensis* did not respond with increased growth when neighboring plants were removed. His research with *Sarracenia rubra* spp. *alabamensis* (Brewer 2005) and *Sarracenia alata* (Brewer 1999) suggested that these carnivorous species may best be considered as a unique class of stress tolerators with phenotypic plasticity constrained by the carnivorous habit (i.e., the same structure functions in photosynthesis and nutrient acquisition). Zamora et al. (1998) studied another carnivorous species, *Pinguicula vallisneriifolia* Webb, and found similar limitations to plasticity with the conclusion that persistence in unfavorable conditions is an important life history trait.

Schulze et al. (2001), without studying demography or habitat variation, predicted local extinction of *Dionaea muscipula* if fire did not occur. They hypothesized that competing vegetation in *D. muscipula* habitats would eventually lead to light limitation, limited trap size, and insect limitation. While it is clear that large fires and the resulting high light conditions at the soil surface will lead to flowering and seedling establishment in *D. muscipula*, it is less clear how developing vegetation affects growth and demography. The fire-free period may be critical for seedling survival and growth particularly in habitats where moisture conditions are marginal. And, a long fire-free period may also eventually produce a large population of dormant plants that can emerge and flower en masse when a fire or clearing event does occur (Luken 2005a). A critical question is how long the species can persist in a dormant condition. This study shows that habitats of *D. muscipula* are defined by a complex interaction among fire, vegetation development and soil moisture. Consistent soil moisture appears to be critical but the species has adaptations that allow persistence across a wide range of vegetation trajectories.

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