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GENETIC STRUCTURE OF TWO ENDANGERED PITCHER PLANTS, *SARRACENIA JONESII* AND *SARRACENIA OREOPHILA* (SARRACENIACEAE)[1]

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Sarracenia jonesii and *S. oreophila* are insectivorous perennial plants of the southeastern United States. Both pitcher plant taxa are rare and endangered. Allozyme diversity was assessed for eight of the ten extant populations of *S. jonesii* and 14 of the 35 remaining *S. oreophila* populations. Genetic diversity was low and comparable for both species (H_{es} = 0.086 and 0.082 for *S. jonesii* and *S. oreophila,* respectively). Mean population genic diversity (H_{ep}) was 0.061 for *S. jonesii* and 0.060 for *S. oreophila.* Estimates of genetic diversity were typical of those commonly associated with endemic species. Small populations of each species and geographically disjunct populations tended to maintain less genetic diversity. Indirect estimates of gene flow were comparable for *S. oreophila* (Nm = 1.62) and *S. jonesii* (Nm = 1.07).

Key words: allozymes; conservation; endangered plants; genetic diversity; pitcher plants; *Sarracenia jonesii*; *Sarracenia oreophila*; Sarraceniaceae.

Botanists and plant enthusiasts have long been fascinated by plants with unusual features. The adaptations of carnivorous plants (species that obtain a portion of their nutrition from another trophic level) have been particularly captivating. In North America, carnivorous plant species occur within the families Droseraceae, Lentibulariaceae, and Sarraceniaceae and include the commonly recognized sundews, the Venus flytrap, the bladderworts, and the pitcher plants, whose highly modified tubular leaves are adapted for catching and digesting insects (Lloyd, 1942). Plant carnivory is thought to be primarily an adaptation to nutrient-poor soils (Schnell, 1976). In the United States, most native carnivorous plants occur in acidic bogs and wetland habitats. The loss and alteration of such habitats have had a profound impact on wetland species throughout the continent (Niering, 1988; Mitsch and Gosselink, 1993; Murdock, 1994).

In the southeastern United States, two pitcher plants, *Sarracenia jonesii* Wherry (Sarraceniaceae) and *S. oreophila* (Kearney) Wherry, have been placed on the federal Endangered Species List. The highly unusual and attractive leaf and floral characteristics of these particular pitcher plants are striking. Unfortunately, the fragile existence of these two species in the wild is jeopardized in part by the very individuals that admire and covet them (U.S. Fish and Wildlife Service, 1990, 1994). The desire of plant enthusiasts to obtain these rare plants imperils the species and may even determine their ultimate fate. The demise of these peculiar species in the wild would represent a loss of biotic uniqueness and natural beauty that could not be fully regained through ex situ conservation. Furthermore, the loss of pitcher plant populations could have detrimental effects on several insect taxa and may even jeopardize the existence of some (U.S. Fish and Wildlife Service, 1990, 1994). The most obvious insect taxa associated with pitcher plants are prey species and pollinators. However, a variety of insect taxa inhabit pitchers and feed on particulate matter in pitcher fluid (Rymal and Folkerts, 1982). Other insect species are herbivores on pitcher plants, including host-specific moth species of the genus *Exyra* (Rymal and Folkerts, 1982). The complex plant/animal interactions that occur within the microcosm of pitcher leaves and at pitcher flowers cannot be duplicated ex situ.

In this study we describe amounts and patterns of genetic variation in populations of *S. jonesii* and *S. oreophila.* Our goal was to provide baseline genetic information pertinent to the conservation and restoration of these species.

SPECIES DESCRIPTIONS

Sarracenia oreophila, the green pitcher plant, is a carnivorous perennial herb with hollow pitcher leaves. Pitchers are tall (20–75 cm long), and range in color from green to yellow-green to deep maroon, with occasional maroon venation. Yellow flowers are borne on scapes 45–70 cm long. *Sarracenia oreophila* flowers have a sweet musty odor (Schnell, 1976) and are pollinated by queens of the genus *Bombus* (U.S. Fish and Wildlife Service, 1994). Pitchers senesce in late summer, when thick, flattened green basal leaves (phyllodia) appear, which persist until the following season.

Sarracenia oreophila, listed as endangered under the federal Endangered Species Act in 1979, historically grew in four states: Alabama, Georgia, North Carolina, and Tennessee (U.S. Fish and Wildlife Service, 1994). Principal habitat of the green pitcher plant is the Cum-

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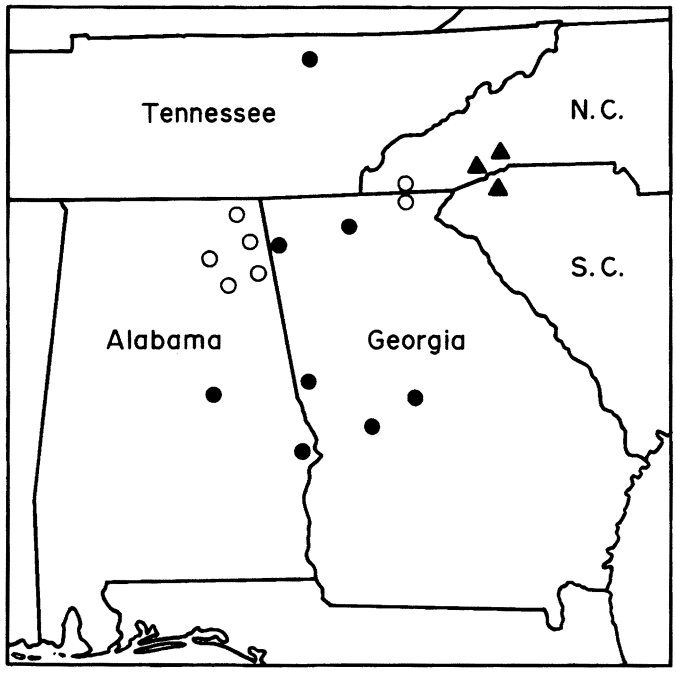

Fig. 1. County locations of *Sarracenia* populations. The triangles indicate the range of *S. jonesii,* open circles and closed circles indicate extant and historic sites, respectively, for *S. oreophila.*

berland Plateau of northeastern Alabama (U.S. Fish and Wildlife Service, 1994) where the species is found in moist upland areas and along stream edges. Historically, fire may have played a role in the maintenance of *S. oreophila* habitat by inhibiting the invasion of woody species. In addition to fire suppression, rural and agricultural development and the collection of plants have probably contributed to its decline (U.S. Fish and Wildlife Service, 1994). At least one insect, the herbivorous moth *Exyra semicrocea,* is host specific to *S. oreophila* (Folkerts, 1992).

Currently, *Sarracenia oreophila* is restricted to 35 sites, 33 of which are in northeastern Alabama (Fig. 1; U.S. Fish and Wildlife Service, 1994). Georgia and North Carolina each harbor one population. Of the 35 extant populations, all but three are located on private lands, and over half are small, numbering fewer than 50 individuals (U.S. Fish and Wildlife Service, 1994). Five populations consist of 500 or more individuals (U.S. Fish and Wildlife Service, 1994).

Both *Sarracenia oreophila* and *S. jonesii* reproduce vegetatively via short rhizomes and sexually from seeds. Asexual reproduction appears to predominate in the species, and rhizomes are reportedly long lived (McDaniel, 1971; Troup and McDaniel, 1980).

Sarracenia jonesii, the mountain sweet pitcher plant, is known from ten populations, four in North Carolina and six in South Carolina (Fig. 1; U.S. Fish and Wildlife Service, 1990). Most populations are small, and only four are protected by state (South Carolina) ownership. Sixteen populations have been extirpated (U.S. Fish and Wildlife Service, 1990). Because of its extreme vulnerability, *S. jonesii* was listed as federally endangered in 1988.

The taxonomic status of *S. jonesii* has been a matter of dispute. It has been variously classified as a regional variant, a form, a subspecies of *S. rubra,* and a distinct species (see Benjamin and Sutter, 1993a for a review). The most recent treatment (McDaniel, 1986) grants species status to the taxon. Supporting this treatment is its disjunct distribution from other species in the *S. rubra* complex, the maintenance of morphological integrity in a common garden, and the unique fragrance and color of the species, which suggests adaptation to a different insect fauna (Benjamin and Sutter, 1993a).

Sarracenia jonesii pitchers are hollow and tubular, and range in height from 21 to 73 cm. The green pitchers are usually partially filled with liquid and decaying insects. The fragrant flowers are (usually) maroon and are borne singly on erect scapes from April through June, with seed set occurring in August (Massey et al., 1983). The habitat of mountain sweet pitcher plant includes depression bogs and cataract bogs (Benjamin and Sutter, 1993a, b). In cataract bogs wetland species line the precipitous sides of waterfalls on granite rock faces and also occur on soil islands on the rocks. Depression bogs have flat to gently sloping topography in valley bottoms that do not flood and are fed by seepages.

MATERIALS AND METHODS

Fourteen populations (one each from Georgia and North Carolina and 12 from Alabama) were sampled across the range of *S. oreophila* in late summer of 1993. Eight *S. jonesii* populations (four each from North and South Carolina) were sampled. Small portions of 48 pitchers were sampled in each population, except for *S. oreophila* populations DK7 (40 leaves), DK5 (28 leaves), and DK8/21 (96 leaves). *Sarracenia jonesii* population STON consisted of samples of five of the remaining six clones being maintained at the Atlanta Botanical Garden. For field collections, pitchers from different clumps of plants were sampled whenever possible. In several *S. oreophila* populations most of the pitchers had senesced, and phyllodia (basal leaves) were sampled. Leaf samples were crushed under liquid nitrogen using a mortar and pestle. An extraction buffer (Mitton et al., 1979) was added to the resultant powder to solubilize and stabilize the enzymes. Leaf extracts were adsorbed onto wicks that were stored in an ultracold freezer (−70°C) until analyzed.

Standard starch gel electrophoresis was employed to analyze the samples. A subset of the following enzymes were stained for each species: amino acid transferase (AAT), aldolase (ALD), diaphorase (DIA), fluorescent esterase (FE), glucose-6-phosphate dehydrogenase (G6PDH), glutamate dehydrogenase (GDH), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), malic enzyme (ME), menadione reductase (MNR), mannose phosphate isomerase (MPI), 6-phosphogluconate dehydrogenase (6-PGDH), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), shikimic dehydrogenase (SKDH), and triose phosphate isomerase (TPI). Enzyme stain recipes were taken from Soltis et al. (1983), except for AAT, DIA, and MNR (Cheliak and Pitel, 1984). The following buffers (numbers refer to Table 1 in Soltis et al., 1983) were used to resolve *S. oreophila* enzymes: Buffer 4 (ALD, IDH, and SKDH), Buffer 6 (PGI, TPI, GDH, ME, MDH, and G6PDH), Buffer 7 (DIA), a modified Buffer 8 (FE), Buffer 10 (AAT), and Buffer 11 (6-PGDH and MPI). For *S. jonesii* we used the following buffer systems: Buffer 4 (ALD, IDH, and SKDH), Buffer 6 (PGI and TPI), a modified Buffer 8 (AAT, DIA, FE, ME, and MNR), and Buffer 11 (6-PGDH and MDH).

A statistical program developed by M.D. Loveless and A. Schnabel was used to analyze the genetic results. Measures of genetic diversity were calculated for each population (Hedrick, 1985) and species (Ham-

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TABLE 1. Species variation and mean population genetic diversity for *Sarracenia jonesii* and *S. oreophila* compared to endemics and short-lived herbaceous species. *P* is the percent polymorphic loci, *AP* is the mean number of alleles per polymorphic locus, *A* is the mean number of alleles per locus, A_e is the effective number of alleles, H_e is gene diversity, or expected heterozygosity, and H_o is observed heterozygosity. Measures subscripted with an *s* indicate species values, while those subscripted with a *p* are population means.

Species	P_s	AP_s	A_s	A_{es}	H_{es}	
Overall total species variation						
Sarracenia jonesii	60.9	2.71	2.04	1.14	0.086	
Sarracenia oreophila	59.1	2.54	1.91	1.15	0.082	
Endemics (159)[a]	43.8	2.99	1.88	1.16	0.110	
Short-lived herbs (236)[a]	45.0	2.73	1.78	1.18	0.136	
Mean population variation	P_p	AP_p	A_p	A_{ep}	H_o	H_{ep}
Sarracenia jonesii	28.3	2.15	1.33	1.10	0.062	0.061
(SD)	(3.3)	(0.02)	(0.11)	(0.17)	(0.013)	(0.010)
Sarracenia oreophila	27.8	2.22	1.34	1.11	0.063	0.060
(SD)	(2.5)	(0.17)	(0.14)	(0.07)	(0.007)	(0.008)
Endemics (159)[a]	29.2	2.58	1.43	1.10	—	0.074
Short-lived herbs (236)[a]	29.0	2.39	1.41	1.13	—	0.103

[a] Unpublished data; updated from Hamrick and Godt, 1989.

rick and Godt, 1989). Values subscripted with an *s* (e.g., H_{es}) refer to species measures, while those with a *p* subscript indicate population measures (e.g., H_{ep}). Genetic diversity (H_T) was calculated for each polymorphic locus and partitioned into that found within populations (H_S) and among populations (D_{ST}; Nei, 1973, 1977). The proportion of total genetic variation found among populations (G_{ST}) was calculated for each polymorphic locus [$G_{ST} = (H_T - H_S)/H_T$] and averaged across variable loci. The statistical significance of G_{ST} values at each locus was calculated using a chi-square test (Workman and Niswander, 1970). Nei's genetic distance (*D*) and identity (*I*) measures (Nei, 1972) were calculated for all conspecific population pairs. A UPGMA cluster analysis of genetic distance values [$D = -\ln(I)$] was generated for each species to examine patterns of genetic association among populations.

Deviations from Hardy–Weinberg expectations were examined by calculating Wright's inbreeding coefficient (*F*) for each locus within populations (Wright, 1922), and tested for significance using chi-square tests (Li and Horvitz, 1953). Outcrossing rates (*t*) were estimated assuming mating system equilibrium (Hedrick, 1985) using the equation $F_e = (1 + t)/(1 - t)$ where F_{IS} was used to estimate the overall inbreeding coefficient (F_e). F_{IS} is the fixation index over all populations (Wright, 1965).

Estimates of gene flow were obtained by calculating *Nm* values (where *Nm* indicates the number of migrants per generation) using Wright's (1931) and Slatkin's (Slatkin, 1985; Barton and Slatkin, 1986) equations. Wright's estimate of gene flow is derived from the proportion of genetic variation found among populations (G_{ST}) and thus is a function of overall allele frequency differences between populations. Slatkin's empirically derived equation for gene flow is based on the frequency of alleles found only in a single population ("private alleles").

RESULTS

Comparable levels of genetic diversity were observed in *S. jonesii* and *S. oreophila* (Table 1). Twenty-three loci were resolved for *S. jonesii,* and 22 for *S. oreophila.* Of these, 61% (14) were variable in *S. jonesii,* with a mean of 2.71 alleles per polymorphic locus, while 59% (13) of the loci examined for *S. oreophila* were variable, with a mean of 2.54 alleles per polymorphic locus. Species-level genetic diversity (H_{es}) was similar for the two species (H_{es} = 0.086 for *S. jonesii,* and 0.082 for *S. oreophila*).

Mean population variation was also comparable for the two pitcher plant taxa. The mean percent polymorphic loci (P_p), the mean number of alleles per variable locus (AP_p), and mean genetic diversity (H_{ep}) values for *S. jonesii* were 28%, 2.15, and 0.061, respectively. The corresponding values for *S. oreophila* were strikingly similar (P_p = 28%; AP_p = 2.22, and H_{ep} = 0.060).

Among *S. jonesii* populations, genetic diversity varied considerably (Table 2). For instance, the percent poly-

TABLE 2. Genetic diversity statistics for *Sarracenia jonesii* and *S. oreophila* populations. P_p is the percent polymorphic loci, AP_p is the mean number of alleles per polymorphic locus, A_p is the mean number of alleles per locus, A_{ep} is the effective number of alleles, H_o is observed heterozygosity, and H_{ep} is gene diversity, or expected heterozygosity. SD is the standard deviation.

A) *Sarracenia jonesii* Population	P_p	AP_p	A_p	A_{ep}	H_o (SD)	H_{ep} (SD)
South Carolina						
ASHW	34.8	2.13	1.39	1.09	0.057 (0.027)	0.059 (0.025)
ASHL	50.0	2.18	1.59	1.08	0.048 (0.031)	0.063 (0.021)
ASHA	28.6	2.17	1.33	1.06	0.034 (0.025)	0.046 (0.021)
CHAN	31.8	2.29	1.41	1.12	0.077 (0.030)	0.072 (0.031)
North Carolina						
KING	39.1	2.22	1.48	1.10	0.063 (0.031)	0.072 (0.026)
KANU	9.1	2.00	1.09	1.08	0.043 (0.022)	0.043 (0.029)
MCCL	19.1	2.25	1.24	1.14	0.070 (0.027)	0.070 (0.037)
STON	14.3	2.00	1.14	1.12	0.106 (0.068)	0.064 (0.035)
B) *Sarracenia oreophila* Population	P_p	AP_p	A_p	A_{ep}	H_o (SD)	H_{ep} (SD)
Alabama						
CK9	23.8	2.40	1.33	1.10	0.060 (0.019)	0.045 (0.030)
DK8/21	33.3	2.29	1.43	1.08	0.049 (0.020)	0.050 (0.026)
DK25	28.6	2.00	1.29	1.08	0.053 (0.025)	0.049 (0.029)
MR7	42.9	2.44	1.62	1.22	0.100 (0.037)	0.113 (0.043)
MR6	35.0	2.43	1.50	1.19	0.091 (0.035)	0.101 (0.041)
CK7	33.3	2.29	1.43	1.20	0.104 (0.035)	0.106 (0.042)
CK10	47.6	2.10	1.52	1.21	0.121 (0.037)	0.117 (0.041)
DK7	28.6	2.00	1.29	1.05	0.043 (0.030)	0.039 (0.016)
DK24	23.8	2.40	1.33	1.06	0.046 (0.025)	0.042 (0.024)
DK9	27.3	2.17	1.32	1.08	0.063 (0.026)	0.048 (0.027)
DK13	18.2	2.25	1.23	1.06	0.036 (0.023)	0.041 (0.023)
DK5	9.1	2.00	1.09	1.06	0.055 (0.023)	0.035 (0.025)
Georgia						
GA	19.1	2.25	1.24	1.03	0.027 (0.021)	0.028 (0.015)
North Carolina						
NC	18.2	2.00	1.18	1.05	0.033 (0.020)	0.032 (0.023)

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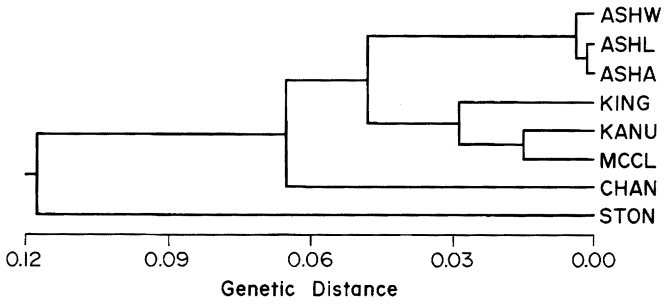

Fig. 2. UPGMA phenogram of genetic distances between *S. jonesii* populations.

TABLE 3. Nei's genetic diversity statistics and estimates of gene flow in two endangered *Sarracenia* taxa. Total genetic diversity (H_T), genetic diversity found within populations (H_S), and the proportion of total genetic diversity found among populations (G_{ST}) were calculated for the variable loci. *Nm* indicates the number of migrants per generation and has been calculated using Wright's equation [Wright, 1931; *Nm*(*W*)] and Slatkin and Barton's (1989) equation [*Nm*(*S*)] with the number of "private" alleles noted in parentheses.

Species	H_T	H_S	G_{ST}	*Nm*(*W*)	*Nm*(*S*)
Sarracenia jonesii	0.142	0.096	0.190	1.07	0.13 (10)
Sarracenia oreophila	0.139	0.100	0.133	1.62	2.56 (6)
Endemics (52)[a]	0.263	0.163	0.248	1.96	1.58

[a] Data from Hamrick and Godt (1989) and Hamrick, Godt, and Sherman-Broyles (1995).

morphic loci ranged from 9% (KANU) to 50% (ASHL), while genetic diversity (H_{ep}) ranged from 0.043 (KANU) to 0.072 (CHAN and KING). Genotype frequencies differed significantly ($P < 0.05$) from Hardy–Weinberg expectations at 11 of the 49 loci tested. All but one of these deviations were positive, indicating heterozygote deficits. Overall, however, the low mean F_{IS} value (0.04) suggested that the species was an outcrosser (estimated t = 0.92).

Significant differences in allele frequencies ($P < 0.001$) among *S. jonesii* populations were found for ten of the 14 polymorphic loci. Overall genetic diversity was low (mean $H_T < 0.01$) at the four loci that did not differ in allele frequencies among populations. Genetic identities between population pairs ranged from 0.859 (ASHL and STON) to 0.999 (ASHL and ASHA). Mean genetic identity between all population pairs was 0.94 (SD = 0.04). When the small population STON was omitted from the analysis, the lowest genetic identity was 0.93 (CHAN with ASHW, ASHL, and ASHA all having the same value) while mean genetic identity rose to 0.96 (SD = 0.02). The correlation between genetic and geographic distance (calculated without STON) was not significant (r = 0.27, P = 0.24). A UPGMA phenogram constructed to examine patterns of relatedness between populations within the species grouped some nearby populations (e.g., ASHW, ASHL and ASHA; MCCL and KANU) but exhibited some anomalies (Fig. 2). In particular, except for STON, CHAN was most distinct, although it is geographically closest to ASHW, ASHL, and ASHA.

A fairly high number of alleles (ten) exclusive to single populations with a mean frequency of 0.22 led to a low estimate of gene flow [*Nm*(*S*) = 0.13] for *S. jonesii* (Table 3). The level of gene flow based on allele frequencies within the entire data set was considerably higher [*Nm*(*W*) = 1.07]. Overall, population divergence was moderate, with 19% of the total genetic variation being found among populations (Table 3).

The range in genetic diversity exhibited by *S. oreophila* populations was somewhat higher than that found for *S. jonesii* (Table 2). For *S. oreophila,* the percent polymorphic loci ranged from 9% (DK9) to 48% (CK10). Genetic diversity varied fourfold among populations, with GA maintaining the lowest diversity (0.028) and CK10 the highest (0.117). Genotype frequencies differed from Hardy–Weinberg expectations at nine of the 81 loci tested. Five of these deviations were negative, indicating heterozygote excesses and four were positive, indicating heterozygote deficiencies. The mean F_{IS} value for *S. oreophila* was −0.04, indicating that the species is outcrossing (estimated t = 1.07).

A moderate level of divergence was observed among *S. oreophila* populations. Although populations differed significantly ($P < 0.05$) in allele frequencies at ten of the 13 polymorphic loci, a relatively small proportion of the total genetic diversity (13.3%) was found among populations (Table 3). Genetic identity values ranged from 0.908 (MR6 and DK9) to 0.997 (DK24 and DK7) with a mean of 0.963 (SD = 0.022). Estimates of gene flow (Table 3) ranged from *Nm*(*S*) = 2.56, based on six "private" alleles to *Nm*(*W*) = 1.62, based on overall population divergence (G_{ST}).

When all *S. oreophila* populations were considered, the correlation between genetic and geographic distance was not significant (r = −0.07; P = 0.49). However, when the highly disjunct Georgia and North Carolina populations (≈ 250 km distant) were omitted the correlation was highly significant (r = 0.42; P = 0.0009). This association is reflected in the UPGMA phenogram (Fig. 3), which clusters many adjacent populations. In particular, if one ignores the Georgia and North Carolina populations, near-neighboring populations tend to be paired (e.g., CK9 and DK8/21; DK7 and DK24; CK7 and CK10; MR7 and MR6). These population pairs were on average <3 km apart (except for DK7 and DK24; 22 km), whereas the mean distance between the Alabama populations was 37 km (range = 1–82 km). The Georgia

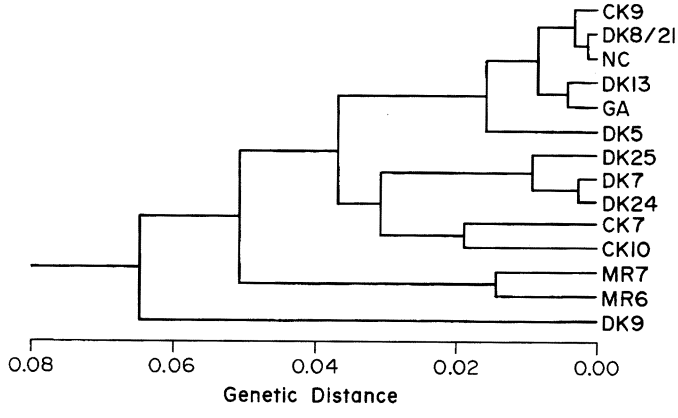

Fig. 3. UPGMA phenogram of genetic distances between *S. oreophila* populations.

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and North Carolina populations, <2 km apart, group fairly close together.

DISCUSSION

Genetic diversity—Allozyme diversity was low within both endangered *Sarracenia* taxa. Low levels of genetic variation can be attributed to a myriad of evolutionary processes acting singly or in concert. For instance, new taxa may acquire a small fraction of the genetic diversity present in their progenitor species (Loveless and Hamrick, 1988; Cole and Biesboer, 1992; Purdy, Bayer, and MacDonald, 1994; Purdy and Bayer, 1995). Drastic range retractions or reductions in species' numbers may also lead to low levels of variation or the lack of allozyme variation (Bonnell and Selander, 1974; Fowler and Morris, 1977; Simon, Bergeron, and Gagnon, 1986; O'Brien et al., 1987; Zabinski, 1992). Species on the federal Endangered Species List have usually experienced reductions in population numbers and sizes as well as habitat loss, often associated with increased geographic isolation. Such ecological events may contribute to the loss of genetic diversity with endangered species harboring mere remnants of their original genetic diversity. Inferences as to the cause(s) of low genetic diversity are frequently difficult to make. However, comparisons with species having similar life history traits, particularly congeners, can provide some insights (Loveless and Hamrick, 1988; Sherman-Broyles et al., 1992; Purdy, Bayer, and MacDonald, 1994). Within the genus *Sarracenia,* genetic diversity is higher for the widespread *S. purpurea* compared to *S. jonesii* and *S. oreophila. Sarracenia purpurea* is found from Florida to Labrador and west to British Columbia. In an analysis of ten allozyme loci for 11 widely scattered *S. purpurea* populations, Schwaegerle and Schaal (1979) found P_s = 50.0% and H_{es} = 0.110. These values compare to P_s = 60.9 and H_{es} = 0.086 for *S. jonesii* and P_s = 59.1 and H_{es} = 0.082 for *S. oreophila.* The higher percent polymorphic loci found for *S. jonesii* and *S. oreophila* coupled with lower H_{es} values indicate that they harbor a higher proportion of low frequency alleles. *Sarracenia purpurea* populations also maintained somewhat higher levels of genetic diversity (mean H_{ep} = 0.095; Schwaegerle and Schaal, 1979) relative to *S. jonesii* and *S. oreophila* (mean H_{ep} = 0.061 and 0.060, respectively). The somewhat lower genetic diversity found in the two endangered species relative to a widespread congener conforms to the pattern documented for several other plant genera (Karron, 1987; Karron et al., 1988). Exceptions to this pattern, however, emphasize the importance of historical events and the need for empirical data (Linhart and Premoli, 1993; Cosner and Crawford, 1994; Lewis and Crawford, 1995).

Species with limited ranges often maintain less genetic diversity than species with widespread distributions (Table 1; Hamrick and Godt, 1989). These two *Sarracenia* species should be classed as "endemics" with regard to geographic range (Hamrick and Godt, 1989; Hamrick, Godt, and Sherman-Broyles, 1995), and thus the low levels of genetic diversity observed within the species were not unexpected. In contrast, the genetic diversity reported for *S. purpurea* is low for a widespread species. For instance, mean H_{es} = 0.150 and mean H_{ep} = 0.118 for species with distributions similar to that of *S. purpurea* (Hamrick and Godt, 1989). Overall, this suggests that the genus *Sarracenia* may be relatively genetically depauperate, perhaps due to the discontinuous distributions that characterize most of its species.

Mating system—Although deviations from Hardy–Weinberg expectations were found for several loci indicating heterozygote deficiencies at some loci and excesses at others, the overall inbreeding coefficients (F_{IS}) suggest that these pitcher plants are highly outcrossed. To our knowledge, quantitative analyses of the mating systems of these species are not available, although viable seeds have resulted from artificial self-pollination of other *Sarracenia* species (Schnell, 1976). Field observations and examinations of *Sarracenia* floral architecture suggest that bees enter the complex flower through a visible parting of the pendulous petal curtains. The pollinator then crosses one of the v-shaped stigmas on one of the five points of the style, which resembles an open, inverted umbrella (Schnell, 1976). Incoming bees deposit pollen on the stigma and pick up pollen that has fallen to the floor of the cup-like style umbrella. On exiting the flower, bees usually leave by a different route (one offering better footing prior to flight) and thus are unlikely to deposit "self" pollen on the visited plant's stigma (Schnell, 1976; Slack, 1979). Given the similar floral architecture of the *Sarracenia*s, the lower outcrossing estimate found for *S. jonesii* more likely reflects biparental inbreeding (mating between relatives) in its small populations or geitonogamous mating than intrafloral selfing.

Decreases in population size may be of particular concern for these *Sarracenia* species since small populations frequently have increased inbreeding with a resultant increase in homozygosity. Species that typically outcross are often susceptible to inbreeding depression upon selfing (Barrett and Kohn, 1991; Ellstrand and Elam, 1993). Inbreeding depression has been empirically documented for small populations of several plant species (Bijlsma, Ouborg, and Van Treuren, 1994; Heschel and Paige, 1995). To our knowledge, the relative fitness of inbred and outcrossed *Sarracenia* progeny has not been compared.

Patterns of genetic diversity—Moderate levels of genetic differentiation were found among populations of these two *Sarracenia* species. The proportion of genetic diversity found among populations (19.0% for *S. jonesii* and 13.3% for *S. oreophila*) was lower than the mean found for endemic plant species (Table 3), and that found for *S. purpurea* (23%; Schwaegerle and Schaal, 1979). *Sarracenia purpurea* was sampled over a larger geographic range than the endangered pitcher plants, and thus the somewhat higher genetic differentiation found for this species is not surprising. A high number of alleles (ten) of moderate frequencies were restricted to single *S. jonesii* populations, whereas the six alleles found exclusively in single *S. oreophila* populations occurred in relatively low frequencies. Both estimates of gene flow suggest that there is somewhat less gene movement among *S. jonesii* populations compared to *S. oreophila* populations. Estimates of gene flow based on G_{ST} values indicate that historic levels of gene flow were marginally suffi-

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cient (i.e., more than one migrant per generation) to counteract genetic drift.

There was a large range in genetic diversity among *S. oreophila* populations. Lower levels of genetic diversity in *S. oreophila* were associated with small or isolated populations, with the disjunct (and intermediate-sized) Georgia and North Carolina populations maintaining the least genetic diversity. Populations at the margins of species' ranges frequently maintain less genetic diversity than centrally located populations (Furnier and Adams, 1986; Bayer 1991; Godt and Hamrick, 1993), although this is not always the case (Perry and Knowles, 1989; Godt, Hamrick, and Bratton, 1995). Isolation may have exacerbated genetic drift within these disjunct *Sarracenia* populations.

The low but highly significant correlation between geographic and genetic distance for the Alabama populations of *S. oreophila* indicates that isolation by distance has played a role in the genetic structure of this species, with more closely adjacent populations experiencing higher interpopulation pollen and seed movement. Undoubtedly other factors (e.g., founder effects, genetic drift, loss of intervening populations, and [possibly] natural selection) have affected genetic relationships among these populations, and the pattern that exists is a combination of past and current gene flow and these other historical events. Within the Alabama populations sampled, MR7 and MR6 (≈1.3 km apart) are most disjunct (by 63 km) and are among the most distantly joined on the phenogram. Mean distance between population pairs for other Alabama populations ranged from 27 to 39 km. DK9, the most distantly joined and distinct population was a small streamside population, averaging 28 km from the other populations. The nonsignificant correlation between populations when the Georgia and North Carolina populations were included indicates that at long distances factors other than gene flow may predominate in determining the genetic composition of populations.

The smallest Alabama *S. oreophila* populations sampled were DK7, DK5, DK13, and DK9 with a mean genetic diversity of 0.041. Four of the larger populations (CK7, CK10, MR6, and MR7) had higher levels of genetic diversity (mean H_{ep} = 0.108). Genetic diversity within other sampled populations was less than half that found in these four. In several plant species small population sizes are associated with lower levels of allozyme diversity (Van Treuren et al., 1991; Godt, Johnson, and Hamrick, in press), less phenotypic variation (Ouborg, Van Treuren, and Van Damme, 1991) and reduced fitness (Heschel and Paige, 1995). Population size should be considered in devising sampling strategies for ex situ *Sarracenia* propagation and conservation, particularly if there is evidence that smaller populations have reduced fitness.

Two major habitat types (streamsides and flatwoods/bogs) have been distinguished for *S. oreophila.* We found no relationship between habitat type and genetic similarity. The three streamside populations (DK13, DK9, and DK5) sampled were among the smallest populations. Although populations DK13 and DK5 grouped fairly closely on the UPGMA phenogram, population DK9 was distantly joined, and most distinct of all the populations.

Sarracenia jonesii populations were between 0.5 km and a maximum of ≈30 km apart, with all sampled populations within ≈ a 15-km radius. Considering its small geographic range, genetic divergence between populations was fairly high. The UPGMA phenogram grouped the three geographically closest populations together (ASHW, ASHL, and ASHA). The distant placement of CHAN on the phenogram was caused in part by a "private allele" in high frequency at *Tpi-1* and a reversal (relative to other populations) in the common allele at *Ald.* The ten "private alleles" were dispersed among four populations [ASHL (2), CHAN (2), KING (3) and STON (3)], suggesting that no single population was exceptionally isolated.

As with *S. oreophila,* larger *S. jonesii* populations maintained more genetic diversity. Of the North Carolina populations, KING was the largest, and most pristine, followed in size by MCCL. Of the South Carolina populations, CHAN was the largest. Except for STON, which consists of two genetically distinct clones (of five sampled) that differed at two polymorphic loci, KANU was the smallest population. The KANU population is <50 m^2 in area and surrounded by developed landscape. This population had the lowest genetic diversity and, in contrast to the others, had no low-frequency (i.e., $P < 0.05$) alleles. KANU showed signs of decline and over a two-year monitoring period it was the only North Carolina population that did not increase in numbers of pitchers (Benjamin and Sutter, 1993b). Furthermore, many plants were in poor condition, and no seedlings were observed during this time (Benjamin and Sutter, 1993b). The decline of plants within KANU may be associated with habitat deterioration coupled with low evolutionary potential.

Conservation considerations—*Sarracenia jonesii* is particularly vulnerable to extinction. Only four of ten extant populations are legally protected by public (state) ownership. The fates of the remaining six are dependent on private landowners. The *S. jonesii* populations are all within a small geographic area, and hence extremely vulnerable to local catastrophes (e.g., drought). Furthermore, the areal extent of the populations themselves is limited (<50 m^2 for four populations, 100–500 m^2 for three and ≈0.5 ha for two, with one undocumented; Benjamin and Sutter, 1993b). Subtle, small-scale disturbances such as a slight rerouting of the waterflows associated with these populations could easily lead to their demise. An additional complication is that *S. jonesii* appears to be mainly composed of small remnant populations, with many populations consisting merely of a few "clumps" of plants. Seedling establishment was documented in only three of the ten populations monitored over 2 yr (Benjamin and Sutter, 1993b) making the populations particularly vulnerable to demographic stochasticity, which could lead to their extinction. Although the existence of *S. oreophila* is not as precarious as *S. jonesii,* this species could also be easily lost since so few populations have legal protection.

As noted above, a relatively high proportion of the alleles found in populations of these two *Sarracenia* species occurs at frequencies below 0.05 (37 and 27 alleles within *S. oreophila* and *S. jonesii* populations, respectively). Species with such skewed allele frequencies are

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especially vulnerable to the loss of allelic richness due to fluctuations in population numbers (Nei, Maruyama, and Chakraborty, 1975). Furthermore, gene flow is unlikely to ameliorate the loss of genetic diversity due to genetic drift because of the isolation of these populations. The lower levels of genetic diversity observed in smaller populations of these two species is most likely a result of population size reduction in previously more robust populations.

Ex situ efforts need to be undertaken to preserve and multiply specimens of both species. Restoration of extirpated populations should also be considered. Propagation of plants from seeds is preferred, since it would be the least detrimental to the extant populations and would include the widest range of genetic diversity. Optimally, seeds from several individuals from each of the populations should be propagated. However, if widespread sampling and propagation are not possible, the most genetically diverse populations of *S. oreophila* (CK7, CK10, MR6, and MR7) should be sampled. For *S. jonesii* the two more diverse and distinct South Carolina populations (ASHL and CHAN) and the North Carolina populations KING and MCCL should be sampled.

The long-term survival of these species is dependent on habitat conservation. When choices must be made between sites to be preserved, levels of genetic diversity within populations should be considered in determining conservation priorities. Perhaps more than most plant species, the unique characteristics of *Sarracenia*s and their complex community interactions exemplify the importance of habitat preservation and in situ conservation.

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