# Morphological variation in *Sarracenia purpurea* (Sarraceniaceae): geographic, environmental, and taxonomic correlates[1]

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Geographic variation in morphology reflects phenotypic responses to environmental gradients and evolutionary history of populations and species and may indicate local or regional changes in environmental conditions. The pitcher plant (*Sarracenia purpurea*) illustrates these principles. At local scales, its morphology reflects nutrient availability. At points along its broad geographic range (from Florida to northern Canada) morphology has been used to distinguish subspecies and varieties, but there has been no detailed study of the continuum of morphological variation across this entire range. Patterns of morphological variation in *S. purpurea* were characterized as a function of climatic and environmental conditions at 39 sites spanning its range. Differences in pitcher size and shape were strongly correlated with temperature, annual precipitation, and availability of ammonium and calcium in peat pore water. Pitcher shape (lip width, mouth diameter, and pitcher width) in Florida panhandle populations differed significantly from pitcher shape of all other populations, even after accounting for environmental correlations. In contrast, the northern and southern subspecies of *S. purpurea* (the latter exclusive of the Florida panhandle populations) cannot be distinguished based on these morphological measurements alone. These results support a recent proposal that identifies the Florida populations as a distinct species, *Sarracenia rosea*.

**Key words:** carnivorous plants; geography; morphology; phylogeography; *Sarracenia purpurea*; *Sarracenia rosea*.

Geographic variation in plant morphology is a function of phenotypic changes in response to local environmental conditions, genetic variation and evolution among populations, and the biogeographic history of an individual species. Characteristics such as leaf shape are constrained genetically, yet they also can be affected greatly by the local environment in which they develop (Thompson, 1991; Schlichting and Pigliucci, 1998). Morphological variation and geographical separation among populations are also prerequisite to the formation of subspecies and species (Losos and Glor, 2003). Phylogeographic analysis can be used to illuminate the interplay of climate, geographical history, and evolutionary dynamics in generating new taxa (Avise et al., 1987; Templeton et al., 1995; Arbogast and Kenagy, 2001).

The North American pitcher plants in the genus *Sarracenia* exemplify the joint roles of these processes. All of the species are sympatric in the southeastern United States, a hot spot for biological diversity in North America (Peet and Allard, 1993; Donovan et al., 2000; Maskas and Cruzan, 2000). Since the end of the Pleistocene glaciation ca. 10 000 yrs ago, one species, *Sarracenia purpurea* L., has rapidly extended its range much further north, and its range now spans more than 30° of latitude and 70° of longitude. Pitcher morphology varies greatly, both within and among species, reflecting differences among sites in growing conditions (Ellison and Gotelli, 2002;

Schnell, 2002) as well as genetic differentiation (Godt and Hamrick, 1999).

*Sarracenia purpurea* sensu lato (sensu Gleason and Cronquist, 1991) is a long-lived, rosette-forming, perennial carnivorous plant that grows in sphagnum bogs, poor fens, seepage swamps, and pine savannas of the eastern United States and Canada (Schnell, 2002). Its broad geographic range includes the entire coastal plain of the eastern United States (the Florida panhandle to Cape Cod), New England and the northern United States westward through the Great Lakes region, and all of Canada east of the Continental Divide (Schnell, 2002; Buckley et al., 2003). Not surprisingly, there is pronounced morphological variability in *S. purpurea* across its range, and botanists have named two subspecies based on quantitative and qualitative differences in pitcher morphology (Schnell, 1979, 2002).

The two subspecies of *S. purpurea*, *S. purpurea* subsp. *purpurea* and *S. purpurea* subsp. *venosa*, are distinguished by the shape of the pitcher hood, the ratio of pitcher length to the diameter of the pitcher opening, the presence or absence of hairs on the outside of the pitcher, and flower color (Schnell, 2002). The size and shape of pitchers, however, can change dramatically in response to local environmental conditions (Mandossian, 1966; Ellison and Gotelli, 2002), and flower color is variable. Hence, Gleason and Cronquist (1991) did not accept the subspecies distinction and considered these two subspecies to be only geographic varieties.

The geographic boundary separating *S. purpurea* subsp. *purpurea* and *S. purpurea* subsp. *venosa* occurs in southern Delaware and northern Maryland and is defined by the southernmost extent of the Pleistocene glaciation: *S. purpurea* subsp. *purpurea* grows in formerly glaciated areas, whereas *S. purpurea* subsp. *venosa* grows only in unglaciated areas. Historical biogeography suggests that *S. purpurea* subsp. *purpurea* is derived from *S. purpurea* subsp. *venosa*, the former

having colonized northern latitudes after glaciation. Furthermore, allozyme analysis suggests that *S. purpurea* subsp. *venosa* and its varieties are more genetically similar to each other than any of them are to *S. purpurea* subsp. *purpurea* (Godt and Hamrick, 1999).

A disjunct group of populations of *S. purpurea* subsp. *venosa* occurs on the Florida panhandle. This population has been described as a separate variety, *S. purpurea* subsp. *venosa* var. *burkii* Schnell (Schnell, 1993), but based on pitcher morphology, flower color, and height of the flower scape, Naczi et al. (1999) proposed that it be considered an entirely separate species, *S. rosea* Naczi, Case & Case. Further, allozyme analysis illustrates that *S. purpurea* subsp. *venosa* var. *burkii* is genetically distinct from both *S. purpurea* subsp. *purpurea* and *S. purpurea* subsp. *venosa*. Covariance of environmental conditions and morphology has not been assessed for either *S. purpurea* subsp. *venosa* or *S. purpurea* subsp. *venosa* var. *burkii*, in contrast to the detailed work on the covariance between environmental conditions and morphology of *S. purpurea* subsp. *purpurea* (Mandossian, 1966; Ellison and Gotelli, 2002). Taxonomic distinctions that are made based on morphology and do not account for the entire range of variability in a taxon may lead to its being split unnecessarily into multiple taxa.

We characterized patterns of variation in vegetative morphology of *S. purpurea* subsp. *purpurea*, *S. purpurea* subsp. *venosa*, and *S. purpurea* subsp. *venosa* var. *burkii* throughout their range in North America. We used these data, along with detailed environmental measurements, to partition morphological variation among geographic/climatic and environmental factors. We asked three questions:

1. Is the observed morphological variation of northern and southern populations of *S. purpurea* associated with environmental and climatic gradients?
2. Do *S. purpurea* subsp. *venosa* and *S. purpurea* subsp. *venosa* var. *burkii*, like *S. purpurea* subsp. *purpurea*, respond morphologically to local environmental conditions?
3. Are observed patterns of morphological variation concordant with identification of infraspecific taxa based on previous morphological and allozyme analyses, and if taken together, do these data support the recent proposal (Naczi et al., 1999) that *S. purpurea* subsp. *venosa* var. *burkii* be considered a separate species, *S. rosea*?

## MATERIALS AND METHODS

Between 1 May and 14 September 2001, we sampled 39 populations distributed throughout the range of *S. purpurea* (Fig. 1). These populations appeared not to have suffered from significant anthropogenic disturbance. Sampling was timed to occur approximately three weeks after flowering, by which time all plants had begun to produce new pitchers. Thus, within the growing season, southern sites were sampled earlier than northern sites. Site-selection criteria included population size (>50 plants), the likely ability of the population to withstand the damage of destructive sampling, and accessibility; state or local agencies and landowners permitted all collections. Because carnivorous plant collectors and hobbyists have planted *S. purpurea* widely, we sampled only native, rather than introduced (adventive) populations (as determined by local Natural Heritage programs and other authorities). We were unable to sample the other described variety of *S. purpurea*, *S. purpurea* subsp. *venosa* var. *montana* Schnell & Determann, which is a threatened endemic limited in distribution to the Blue Ridge Mountains and adjacent piedmont of southwestern North Carolina, northwestern South Carolina, and northeastern Georgia (Schnell and Determann, 1997). Because we sampled after plants had flowered, we did not collect data on flower color or shape.



Fig. 1. Map of North America showing the 39 sample locations. Symbols indicate described subspecies of *Sarracenia purpurea* (open circles: 27 populations of *S. purpurea* subsp. *purpurea*; solid circles: 7 populations of *S. purpurea* subsp. *venosa*) or 5 populations of *S. purpurea* subsp. *venosa* var. *burkii* (solid triangles).

The latitude, longitude, and elevation of each site were determined using a hand-held GPS (global positioning system) unit accurate to ±50 m. Climatic variables were obtained for each site from the nearest (<100 km) weather stations and included 10-year means of the number of frost days per year; annual precipitation and snowfall; monthly, December minimum, July maximum, annual minimum and annual maximum temperatures; and variance in monthly temperature.

At each site, we laid a 1-m-wide belt transect across the longest axis of the *Sarracenia* population. If this axis was longer than 100 m, we used a 100-m transect centered on this axis. This transect was then divided into 20 equally spaced marks (maximum of 5 m apart), and the nearest pitcher plant to each mark was identified. For each of these 20 plants, we measured the maximum diameter of the rosette. For the first (largest) pitcher of the current year, we measured (±1 mm) the pitcher length, diameter of the pitcher mouth, the thickness of the pitcher lip, the maximum width of the pitcher, and the width of the wing (keel); see Ellison and Gotelli (2002) for an illustration of these measurements. The thickness of the lip of the pitcher and the ratio of pitcher length to mouth diameter have been used as key characters to distinguish among *S. purpurea* subsp. *purpurea*, *S. purpurea* subsp. *venosa*, and *S. purpurea* subsp. *venosa* var. *burkii* (Naczi et al., 1999; Schnell, 2002).

Because size and shape of *S. purpurea* subsp. *purpurea* pitchers are known to vary with light and vegetation cover (Mandossian, 1966), we visually estimated percentage cover of vegetation in a 1-m² quadrat centered on each plant. Because there was no consistent set of co-occurring species across the range of *S. purpurea*, we distinguished percentage cover of functional groups: trees, shrubs, terrestrial or aquatic forbs, graminoids, ferns, lycopods, *Sphagnum*, other bryophytes, fungi, and lichens.

Relative wing width of pitchers (wing width/total pitcher width) previously has been correlated with pore-water nitrogen concentrations (Ellison and Gotelli, 2002). Therefore, we examined covariance between pitcher morphology and nutrient concentrations in pore water. We took five pore-water samples, evenly spaced across the sample transect. Fifty-mL water samples were extracted using clean Tygon tubing from 50 cm long × 2.5 cm diameter capped and perforated PVC tubes that were sunken into the peat. For each sample, we measured pH and calcium (mg/L) with Orion ion-sensitive electrodes (Thermo Electron Corp, Woburn, Massachusetts, USA), and phosphate ($PO_4$-P), nitrate ($NO_3$-N), and ammonium ($NH_4$-N) (all in mg/L) spectrophotometrically using US-EPA standard methods (Bledzki and Ellison, 1998; Clesceri et al., 1998). Pore-water samples were not taken in eight southern sites, due to insufficient water availability in the drier sandy soils.

Some data reduction was performed prior to analysis. First, because the unit of interest was the site ($N = 39$ sites), the relationships between morphology and geographic, environmental, and climatic variables were based on means at each site (of $N = 20$ plants or vegetation samples per site; $N = 5$

TABLE 1. Results of the principal component analysis on the nine climatic variables. The first two principal axes accounted for 96% of the variance in the data. Values shown are the loadings of each variable on each of the first two axes.

| Variable | Axis 1 | Axis 2 |
|---|---|---|
| Frost-free days | 0.357 | −0.128 |
| Annual minimum temperature | −0.361 | 0.150 |
| Annual maximum temperature | −0.366 | 0.051 |
| Mean monthly temperature | −0.365 | 0.098 |
| December minimum temperature | −0.345 | 0.267 |
| July maximum temperature | −0.354 | −0.106 |
| Variance in monthly temperature | 0.330 | −0.290 |
| Mean annual precipitation | 0.260 | 0.583 |
| Mean annual snowfall | 0.231 | 0.665 |
| Cumulative proportion of variance explained | 0.817 | 0.965 |

pore-water samples per site). Because of correlations among climatic variables, among vegetation variables, and among pore-water chemical variables, we performed principal component analysis (PCA) to generate two principal axes that accounted for the majority of variance of each of these sets of predictor variables. All variables were standardized (transformed into standard-deviation units, or $Z$ scores) prior to performing the PCA (Gotelli and Ellison, 2004). We also extracted two principal axes describing pitcher size and shape using PCA on the (similarly standardized) morphological variables measured for each pitcher. We separately analyzed two morphological variables used to separate the subspecies of *S. purpurea* (the width of the pitcher lip and the pitcher length : mouth diameter ratio) and the morphological ratio known to co-vary with pore-water nitrogen concentration (relative wing width).

All morphological variables (principal axis scores or the three distinct variables) were regressed on the environmental predictor variables. Stepwise multiple regression and Akaike's information criterion (AIC: Burnham and Anderson, 2002) were used to identify the best-fitting model and the variables that best predicted pitcher morphology.

Our first two questions addressed geographic and environmental correlates of morphological variability without regard to taxonomic distinctions. Therefore, we initially analyzed the data without classifying the observations according to infraspecific designations. These analyses illustrate patterns of covariance between morphological traits and climate, vegetation, and pore-water chemistry across the entire geographic range of *S. purpurea*.

Our third question asked if observed patterns of morphological variation were concordant with identification of infraspecific taxa by other authors based on morphology. To address this question, we used one-way analysis of variance (ANOVA) to test whether plant morphology (both the principal axis scores and the three distinct morphological variables) differed consistently among *S. purpurea* subsp. *purpurea*, *S. purpurea* subsp. *venosa*, and *S. purpurea* subsp. *venosa* var. *burkii*. In these ANOVAs, taxonomic designation was considered a fixed factor. A priori contrasts were used to test (a) whether *S. purpurea* subsp. *venosa* var. *burkii* differed from the two *S. purpurea* subspecies and (b) whether the two subspecies of *S. purpurea* differed from each other. Last, an analysis of covariance (ANCOVA) was used to determine if morphological differences among infraspecific taxa remained after accounting for covariance between morphological and environmental variables. All data analyses were done using S-Plus version 6.1 (Insightful Corporation, Seattle, Washington, USA).

## RESULTS

***Data reduction through principal component analysis***— Climatic data were well summarized by the first two principal axes (Table 1), which together accounted for 96% of the variation among sites. The first principal axis was strongly correlated with latitude ($r^2 = 0.94$) and reflected temperature differences among the sites (cool, northern sites had high values for this axis). The second principal axis reflected differences in precipitation among the sites (sites receiving more rain and snow had high values for this axis). Southern sites were intermediate in precipitation, whereas differences in precipitation among northern sites were associated with longitude: western sites were drier than eastern sites.

Two principal axes accounted for 60% of the variation in vegetation composition. The first principal axis separated *Sphagnum*-shrub bogs (high values on the axis) from poor fens and seepage swamps with higher densities of graminoids and forbs (low values on the axis). The second axis reflected light available to pitcher plants. Shady sites with many trees or shrubs had high values on this axis, and sunny sites with few trees or shrubs had low values on this axis. Neither of these vegetation axes was correlated with latitude, longitude, or climate.

Data for pore-water chemistry were available for 31 of the 39 sites, and the first two principal axes accounted for 61% of the variation in water chemistry among those sites (Table 2). The first principal axis reflected ammonium and calcium availability (sites with high concentrations of these two ions had large values on this axis), whereas the second principal axis reflected pH and phosphate concentrations (sites with high pH and high $PO_4$ concentrations had large values on this axis). The first principal axis also was correlated with the latitude ($r = 0.60$), illustrating the well-known increase in nitrogen deposition rates at higher latitudes (Ollinger et al., 1993).

The first two principal axes of plant morphology accounted for 81% of the variation among sites (Table 3). The first prin-

TABLE 2. Results of the principal component analysis on the five soil chemistry variables. The first two principal axes accounted for 61% of the variance in the data. Values shown are the loadings of each variable on each of the first two axes.

| Variable | Axis 1 | Axis 2 |
|---|---|---|
| pH | 0.126 | 0.733 |
| $PO_4$ | −0.268 | 0.596 |
| $NH_4$ | 0.649 | −0.007 |
| $NO_3$ | −0.142 | 0.282 |
| $Ca^{+2}$ | 0.686 | 0.164 |
| Cumulative proportion of variance explained | 0.336 | 0.612 |

TABLE 3.   Results of the principal component analysis on the site means of the six morphological variables measured for each plant. The first two principal axes accounted for 81% of the variance in the data. Values shown are the loadings of each variable on each of the first two axes.

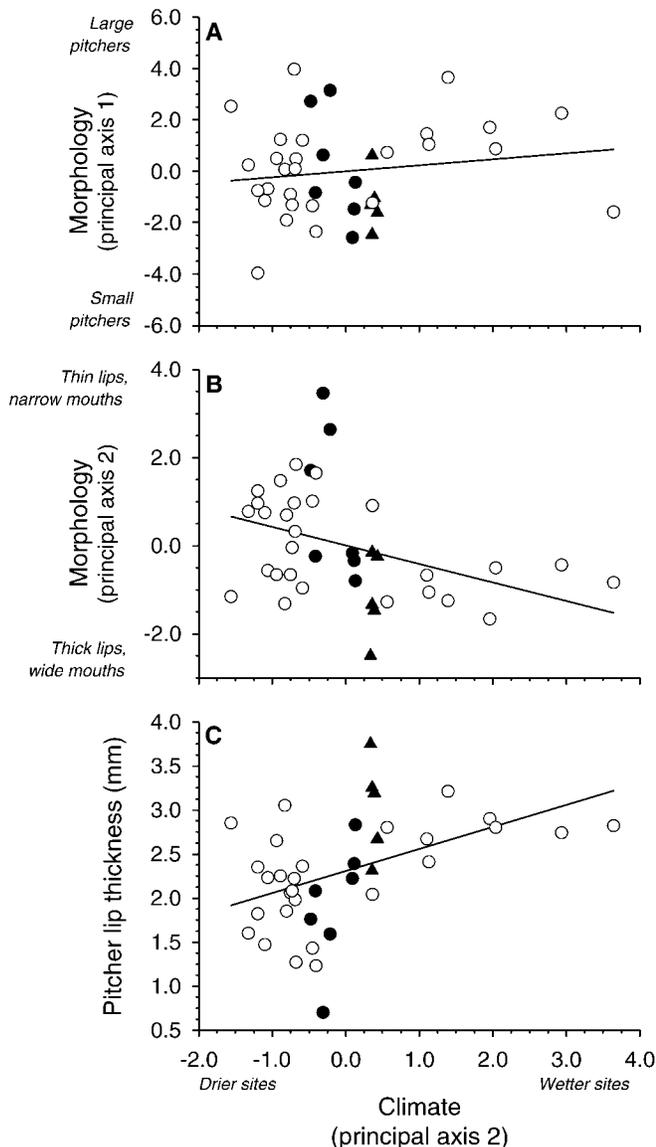| Variable | Axis 1 | Axis 2 |
|---|---|---|
| Rosette diameter | 0.459 | 0.283 |
| Leaf length | 0.498 | −0.001 |
| Mouth diameter | 0.334 | −0.555 |
| Lip thickness | 0.089 | −0.702 |
| Pitcher width | 0.518 | −0.026 |
| Wing width | 0.389 | 0.341 |
| Cumulative proportion of variance explained | 0.490 | 0.755 |



Fig. 2.   Relationship between climate and three measures of pitcher-plant morphology. In all cases, the predictor variable (*x*-axis) is the second principal axis of climate, which is dominated by precipitation (see Table 1 for all loadings). Symbols are as in Fig. 1. The line is the best-fit linear regression. **A.** Pitcher size (the first morphological principal axis: see Table 3 for all loadings) as a function of climate. Slope = 0.22, $r^2$ = 0.21, *P* = 0.049. **B.** Pitcher shape (the second morphological principal axis: see Table 3 for all loadings) as a function of climate. Slope = −0.40, $r^2$ = 0.15, *P* = 0.019. **C.** Lip width alone of pitchers as a function of climate. Slope = 0.21, $r^2$ = 0.20, *P* = 0.005.

cipal axis reflected pitcher size differences (plants with tall and wide pitchers have high values for this axis). The second principal axis reflected differences in pitcher shape (plants with thin lips, narrow mouths, and large wings had large values on this axis).

*Predictors of site-specific morphology*—The first set of analyses was conducted without regard to taxonomic identity. All composite and individual morphological variables were best predicted by climate variables. The second principal axis of climate (dominated by precipitation) was the best predictor of the two morphological principal axes and pitcher lip width (Fig. 2). In general, pitchers from wetter sites were larger (Fig. 2A) and had thicker lips (Fig. 2B, 2C). The length : mouth ratio was inversely related to temperature variables (the first principal axis of climate) (Fig. 3A). Tall pitchers with relatively narrow tubes were more common in warmer, southern sites while shorter, relatively stout pitchers predominated in cooler, northern sites. Relative wing width was marginally correlated only with the first principal axis of pore-water chemistry. Pitchers with relatively large wings occurred in sites with high concentrations of ammonium and calcium in the pore water (Fig. 3B). Neither bog type (vegetation PC-1) nor vegetation stature and composition (PC-2), a proxy for light availability, were correlated with any morphological character.

*Differences among infraspecific taxa*—The primary character that separated *S. purpurea* subsp. *venosa* var. *burkii* from both *S. purpurea* subsp. *purpurea* and *S. purpurea* subsp. *venosa* was the thickness of the pitcher lip (Fig. 2B, 2C; $F_{2,36}$ = 5.39, *P* = 0.009, one-way ANOVA). Based on results of a priori contrasts, *Sarracenia purpurea* subsp. *venosa* var. *burkii* had significantly (*P* = 0.003) thicker lips ($\bar{X}$ = 3.0 ± 0.56 [SD] mm, range 2.3–3.8 mm) than did the two *S. purpurea* subspecies combined (2.2 ± 0.59, range 0.7–3.2 mm), but lip thickness did not differ (*P* = 0.19) between the two subspecies of *S. purpurea* (*S. purpurea* subsp. *purpurea*: 2.3 ± 0.56, range 1.2–2.8 mm; *S. purpurea* subsp. *venosa* excluding *S. purpurea* spp. *venosa* var. *burkii*: 1.9 ± 0.68, range 0.7–2.8 mm). The second principal axis of morphology, for which the loadings (Table 3) were dominated by lip thickness, pitcher mouth diameter, and wing width, also separated these taxa (Fig. 2B; $F_{2,36}$ = 4.37, *P* = 0.02, one-way ANOVA). The results of the a priori contrasts on the second principal axis of morphology were identical to the contrasts on lip thickness alone. *Sarracenia purpurea* subsp. *venosa* var. *burkii* had significantly lower scores (*P* = 0.01) than the two other infraspecific taxa of *S. purpurea* for the second principal axis of morphology, and these morphological features did not differ between the two subspecies of *S. purpurea* (*P* = 0.08). None of the other morphological characters that we measured—
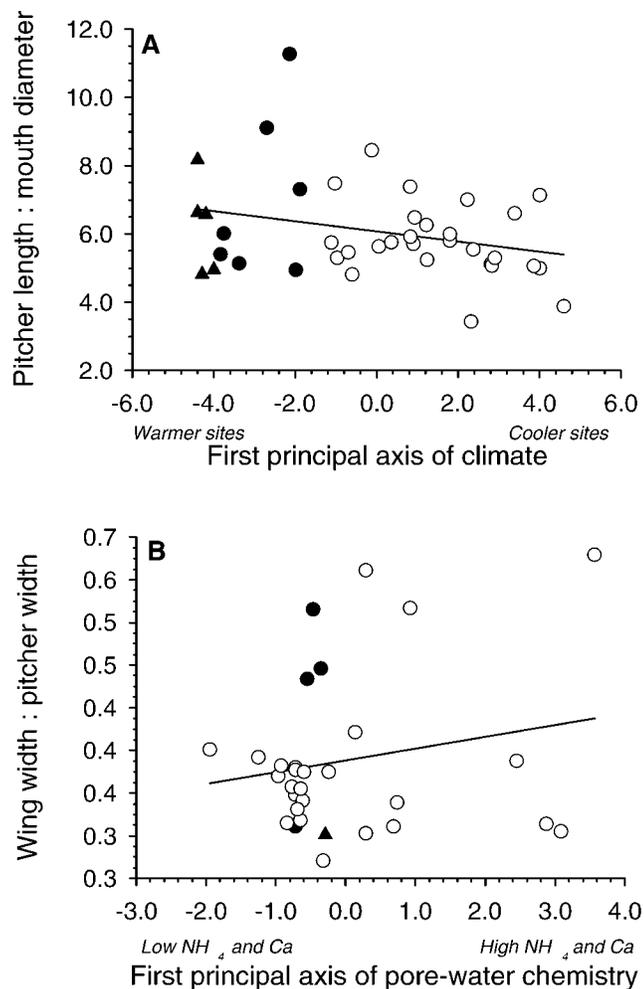
Fig. 3. Relationship between derived measures of pitcher-plant morphology and environmental variables. **A.** The ratio of pitcher length to mouth diameter as a function of the first principal axis of climate (dominated by temperature: see Table 1 for all loadings). Slope $= -0.29$, $r^2 = 0.18$, $P = 0.02$. **B.** The ratio of wing width to total pitcher width as a function of the first principal axis of pore-water chemistry (dominated by $NH_4$ and calcium availability: see Table 2 for all loadings). Slope $= 0.12$, $r^2 = 0.09$, $P = 0.09$. Symbols for both **A** and **B** as in Fig. 1.

pitcher length : mouth diameter ratio (Fig. 3A), relative wing width (Fig. 3B), or the first principal axis of morphology (Fig. 2A)—differed at all among the three taxa ($F_{2,36} = 2.12$, $P = 0.13$; $F_{2,36} = 0.99$, $P = 0.38$; $F_{2,36} = 1.20$, $P = 0.31$, one-way ANOVAs on the three variables, respectively), so we did not examine the contrasts between *S. purpurea* subsp. *venosa* var. *burkii* and *S. purpurea* or between the two subspecies of *S. purpurea*.

The inclusion of either or both of the principal axes of climate as covariates in the analysis of variance (i.e., an AN-COVA) on plant morphology does not alter our conclusions. *Sarracenia purpurea* subsp. *venosa* var. *burkii* still separates out from the two subspecies of *S. purpurea* ($P = 0.004$ for the a priori contrast), and the two subspecies of *S. purpurea* are not distinguishable ($P = 0.86$ for the a priori contrast).

## DISCUSSION

Our results illustrate that morphological variation in *S. purpurea* is associated with environmental conditions, geography, and taxonomic identity. Morphology of the two subspecies of *S. purpurea* is correlated with environmental conditions. Both size and shape of pitchers of *S. purpurea* subsp. *purpurea* and *S. purpurea* subsp. *venosa* are primarily a function of precipitation (the dominant variable loading on the second principal axis of climate), which itself varies consistently with longitude. The primary morphometric ratio used to distinguish between the two subspecies (pitcher length : mouth diameter) covaries with temperature (the dominant variable loading on the first principal axis of climate), which itself is strongly correlated with latitude.

There is some indication that available nutrients may also alter the amount of tissue in the pitcher wing relative to the width of the pitcher itself. Sites with high levels of ammonium and calcium tend to have plants with larger wings and narrower pitchers than do sites with lower levels of these nutrients, although most of the variation among sites remains unexplained. This pattern is consistent with the hypothesis of Givnish et al. (1984) that relative allocation of resources to carnivorous structures results from the "costliness" of producing carnivorous structures. Pitchers with relatively large wings are photosynthetically more efficient than those with relatively small wings (Ellison and Gotelli, 2002) and predominate when more nutrients are available.

Our data illustrate that there is no obvious way to distinguish these subspecies on morphological grounds alone, supporting Gleason and Cronquist's (1991) treatment of these subspecies as simple geographic varieties of *S. purpurea*. The two principal morphological characters used to distinguish *S. purpurea* subsp. *purpurea* from *S. purpurea* subsp. *venosa*, the ratio of pitcher length to mouth diameter and the thickness of the pitcher lip (Schnell, 2002), do not differ between northern and southern populations of *S. purpurea*. Because the two varieties co-occur in the mid-Atlantic states where their ranges overlap, introgression and hybridization are possible (Godt and Hamrick, 1999). Additional genetic analysis (e.g., DNA sequencing) and field investigations of hybridization between *S. p. purpurea* and *S. p. venosa* are needed to resolve their taxonomic status definitively.

Our data do clearly support the differentiation of *S. purpurea* subsp. *venosa* var. *burkii* from *S. purpurea*, however. *Sarracenia purpurea* subsp. *venosa* var. *burkii* differs not only in the morphological characters measured here, but also in pitcher and flower color (Naczi et al., 1999), height of the flower scape (Naczi et al., 1999), and seed size and germination characteristics (Ellison, 2001).

Overall, these conclusions are consistent with earlier results of allozyme analysis (Godt and Hamrick, 1999). *Sarracenia purpurea* subsp. *venosa* var. *burkii* is genetically quite distinct from the recognized infraspecific taxa of *S. purpurea*. *Sarracenia purpurea* subsp. *venosa* and *S. p. purpurea* are genetically similar, and the allozyme data, which suggest that *S. purpurea* subsp. *venosa* is derived relative to *S. purpurea* subsp. *purpurea*, are at odds with the geographic distribution, which suggests that *S. purpurea* subsp. *purpurea* is a postglacial derivative of *S. purpurea* subsp. *venosa*. Godt and Hamrick (1999), also point out that the genetic grouping of *S. purpurea* subsp. *venosa* (and *S. purpurea* subsp. *venosa* var. *montana*) with *S. purpurea* subsp. *purpurea* is not consistent with a taxonomic system that places *S. purpurea* subsp. *venosa* var. *burkii* into *S. purpurea* subsp. *venosa*.

It could be argued that the observed differences between *S. purpurea* subsp. *venosa* var. *burkii* and *S. purpurea* simply

reflect correlated habitat factors because the southern populations are in the warmest sites (Fig. 3A) and are intermediate in precipitation (Fig. 2A). However, including either or both of the principal axes of climate as covariates into an ANCOVA does not alter our conclusions. *Sarracenia purpurea* subsp. *venosa* var. *burkii* remains distinctive from *S. purpurea*, and the subspecies of *S. purpurea* are not separable morphologically. Overall, these results support the recognition of *Sarracenia purpurea* subsp. *venosa* var. *burkii* as the distinct species *S. rosea* (Naczi et al., 1999). Recognition of its status as a distinct species also would facilitate protection of the rare *S. rosea* (Godt and Hamrick, 1999). The comprehensive geographic analysis described herein is a useful tool for understanding morphometric variation and its information value for taxonomic studies.

## LITERATURE CITED

ARBOGAST, B. S., AND G. J. KENAGY. 2001. Comparative phylogeography as an integrative approach to historical biogeography. *Journal of Biogeography* 28: 819–825.

AVISE, J. C., J. ARNOLD, R. M. BALL, E. BERMINHAM, T. LAMB, J. E. NEIGEL, C. A. REEB, AND N. C. SAUNDERS. 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. *Annual Review of Ecology and Systematics* 18: 489–522.

BLEDZKI, L. A., AND A. M. ELLISON. 1998. Population growth and production of *Habrotrocha rosa* Donner (Rotifera: Bdelloidea) and its contribution to the nutrient supply of its host, the northern pitcher plant, *Sarracenia purpurea* L. (Sarraceniaceae). *Hydrobiologia* 385: 193–200.

BUCKLEY, H. L., T. E. MILLER, A. M. ELLISON, AND N. J. GOTELLI. 2003. Reverse latitudinal trends in species richness of pitcher-plant food webs. *Ecology Letters* 6: 825–829.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York, New York, USA.

CLESCERI, L. S., A. E. GREENBERG, AND A. D. EATON. 1998. Standard methods for the examination of water and wastewater, 20th ed. American Public Health Association, Washington, DC, USA.

DONOVAN, M. F., R. D. SEMLITSCH, AND E. J. ROUTMANE. 2000. Biogeography of the southeastern United States: a comparison of salamander phylogeographic studies. *Evolution* 54: 1449–1456.

ELLISON, A. M. 2001. Interspecific and intraspecific variation in seed size and germination requirements of *Sarracenia* (Sarraceniaceae). *American Journal of Botany* 88: 429–437.

ELLISON, A. M., AND N. J. GOTELLI. 2002. Nitrogen availability alters the expression of carnivory in the northern pitcher plant *Sarracenia purpurea*. *Proceedings of the National Academy of Sciences, USA* 99: 4409–4412.

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.

GLEASON, H. A., AND A. CRONQUIST. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. New York Botanical Garden, Bronx, New York, USA.

GODT, M. J. W., AND J. L. HAMRICK. 1999. Genetic divergence among infraspecific taxa of *Sarracenia purpurea*. *Systematic Botany* 23: 427–438.

GOTELLI, N. J., AND A. M. ELLISON. 2004. A primer of ecological statistics. Sinauer Associates, Sunderland, Massachusetts, USA.

LOSOS, J. B., AND R. E. GLOR. 2003. Phylogenetic comparative methods and the geography of speciation. *Trends in Ecology and Evolution* 18: 220–227.

MANDOSSIAN, A. J. 1966. Variations in the leaf of *Sarracenia purpurea* (pitcher plant). *The Michigan Botanist* 5: 26–35.

MASKAS, S. D., AND M. B. CRUZAN. 2000. Patterns of intraspecific diversification in the *Piriqueta caroliniana* complex in southeastern North America and the Bahamas. *Evolution* 54: 815–827.

NACZI, R. F. C., E. M. SOPER, F. W. CASE, JR., AND R. B. CASE. 1999. *Sarracenia rosea* (Sarraceniaceae), a new species of pitcher plant from the southeastern United States. *Sida* 18: 1183–1206.

OLLINGER, S. V., J. D. ABER, G. M. LOVETT, S. E. MILLHAM, R. G. LATHROP, AND J. M. ELLIS. 1993. A spatial model of atmospheric deposition for the northeastern U.S. *Ecological Applications* 3: 459–472.

PEET, R. K., AND D. J. ALLARD. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification. *Proceedings of the Tall Timbers Fire Ecology Conference* 18: 45–81.

SCHLICHTING, C. D., AND M. PIGLIUCCI. 1998. Phenotypic evolution: a reaction norm perspective. Sinauer Associates, Sunderland, Massachusetts, USA.

SCHNELL, D. E. 1979. A critical review of published variants of *Sarracenia purpurea* L. *Castanea* 44: 47–59.

SCHNELL, D. E. 1993. *Sarracenia purpurea* L. subsp. *venosa* (Raf.) Wherry var. *burkii* Schnell (Sarraceniacaea)—a new variety of the Gulf coastal plain. *Rhodora* 95: 6–10.

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

SCHNELL, D. E., AND R. O. DETERMANN. 1997. *Sarracenia purpurea* L. subsp. *venosa* (Raf.) Wherry var. *montana* Schnell & Determann (Sarraceniaceae): a new variety. *Castanea* 62: 60–62.

TEMPLETON, A. R., E. ROUTMAN, AND C. A. PHILLIPS. 1995. Separating population structure from population history: a cladistic analysis of the geographic distribution of mitochondrial DNA haplotypes in the tiger salamander *Ambystoma tigrinum*. *Genetics* 140: 767–782.

THOMPSON, J. D. 1991. Phenotypic plasticity as a component of evolutionary change. *Trends in Ecology and Evolution* 6: 246–249.