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

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*
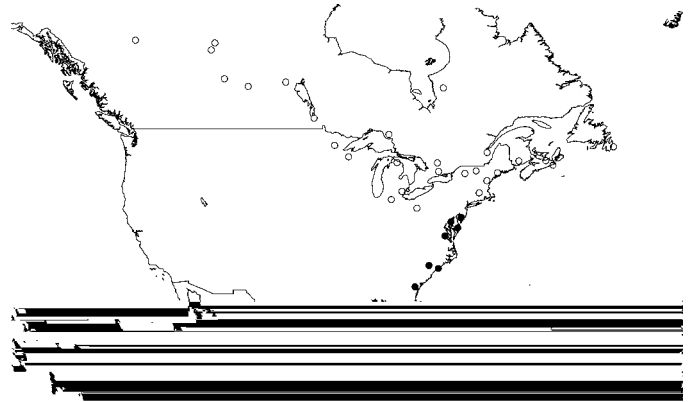

Fig. 1. Map of North America showing the 39 sample locations. Symbols indicate described subspecies of *Sarracenia purpurea* (open circles: 27 populations of *S. purpurea* subsp. *purpurea*; solid circles: 7 populations of *S. purpurea* subsp. *venosa*) or 5 populations of *S. purpurea* subsp. *venosa*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

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

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 mouthps,rec45ge wimshaph values on thihaph oone of piP6(variabe)-38 0 Te-sp6(phoc5T Tf 49t eh)]TJ 6.47 tFig. T2 TIn-275(Tgeneral,-270(sitchers)-280(pfrom-280(pwettr)-25053
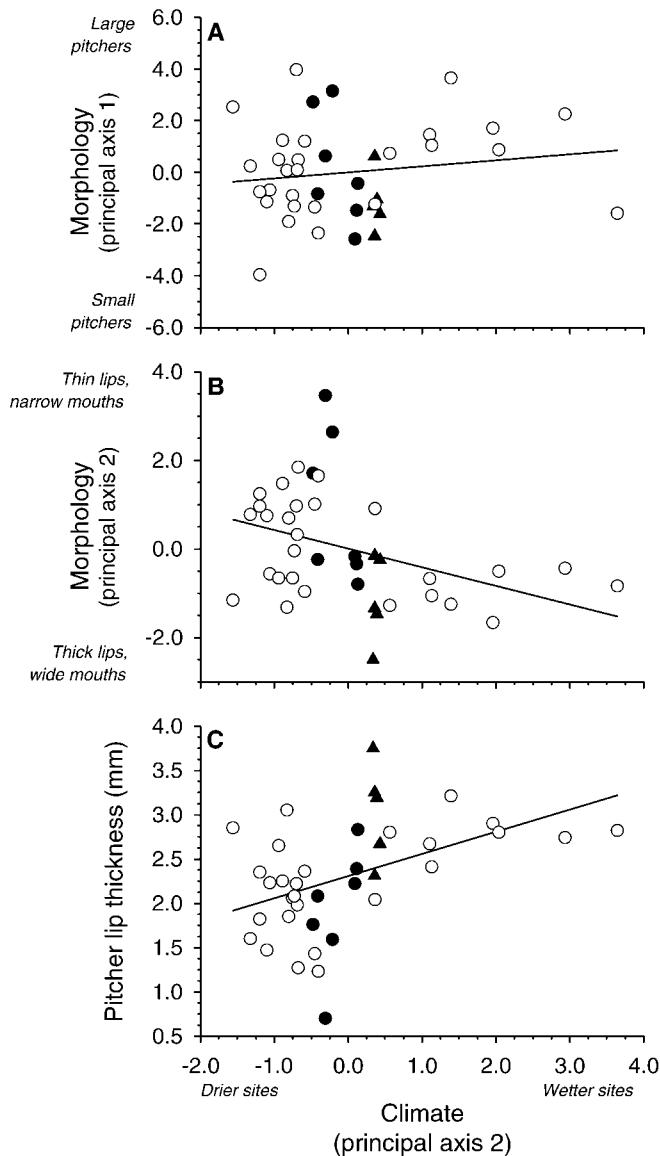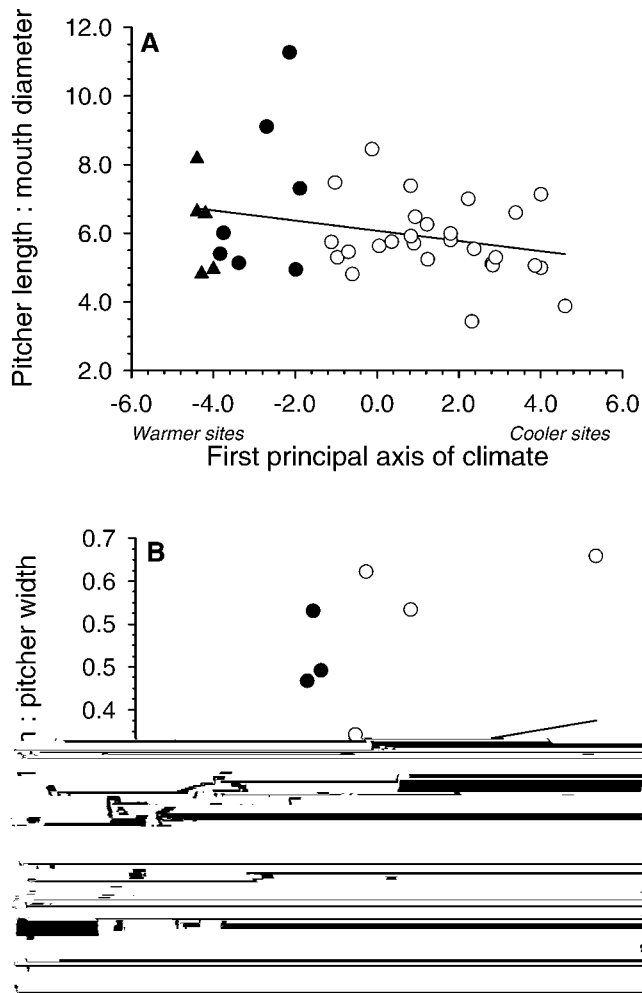

Fig. 2.   Relationship between climate and three measures of pitcher-plant morphology. In all cases, the predictor variable (*x*-axis) is the second principal axis of climate, which is dominated by precipitation (see Table 1 for all loadings). Symbols are as in Fig. 1. The line is the best-fit linear 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.

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 $= -0.29$, $r^2 = 0.18$, $P =$