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Diel Variation of Sugar Amount in Nectar from Pitchers of *Sarracenia purpurea* L. with and without Insect Visitors

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ABSTRACT.—*Sarracenia purpurea* L. is a carnivorous pitcher plant that attracts insect prey by producing nectar. We compared amount of sugar in different samples of nectar collected during the day and night and from bagged and nonbagged pitchers. Sugar content was measured in nectar samples from 87 pitchers at 3 h intervals over a 24 h period through the use of a wick-sampling technique and a colorimetric assay. We monitored environmental conditions at the time of nectar collection and correlated them with the amount of sugar/wick. We also measured ten pitcher characteristics and examined their relationship to variations in 24 h sugar amount. Sugar amount was higher at night for both bagged and nonbagged pitchers. During the day nonbagged pitchers had lower sugar amounts than bagged pitchers, perhaps due to removal of nectar by insects. A similar, but less pronounced, difference was observed at night. Relative humidity, air and ground temperature and time of day had little effect on sugar amount. Our data suggest that nectar may crystallize during the day and dissolve when dew forms at night.

INTRODUCTION

Nectar is an important source of nourishment and water for insects; consequently, it is an effective means of attracting and rewarding pollinators. Nectar studies have examined production patterns (Galetto *et al.*, 1994), sugar composition (Barnes *et al.*, 1995), nonsugar constituents (Baker and Baker, 1983) and the effect of environment on nectar characteristics (Bertsch, 1983; Jakobsen and Kristjánsson, 1994). Many of the factors affecting nectar production have been examined with respect to their ability to attract insects (Erhardt, 1991).

Extra-floral nectar (EFN), produced by nectaries on leaves, petioles, stipules and stems, also attracts insects. EFN, like floral nectar, contains sugars, amino acids and other chemical constituents (Baker *et al.*, 1978; Dress *et al.*, 1997) which provide insects with necessary nutrients and water. EFN appears to reduce herbivory and seed predation (Pemberton and Lee, 1996). Most studies have focused on the mutualistic system between plants and ants whereby ants reduce herbivory by aggressively removing adult herbivores or their eggs or larvae (Bentley, 1977; Stephenson, 1982). Relatively few studies have investigated EFN production patterns, primarily due to the difficulty involved in accurately collecting and measuring nectar (*e.g.*, Wunnacht *et al.*, 1992).

Several types of carnivorous plants, including the various pitcher plant genera *Heliamphora*, *Nepenthes*, *Darlingtonia*, *Cephalotus* and *Sarracenia*, attract prey by EFN production (Juniper *et al.*, 1989). Nectar is a useful attractant because of its energetic value to insects, which is primarily a function of its caloric or carbohydrate content. Although EFN has been

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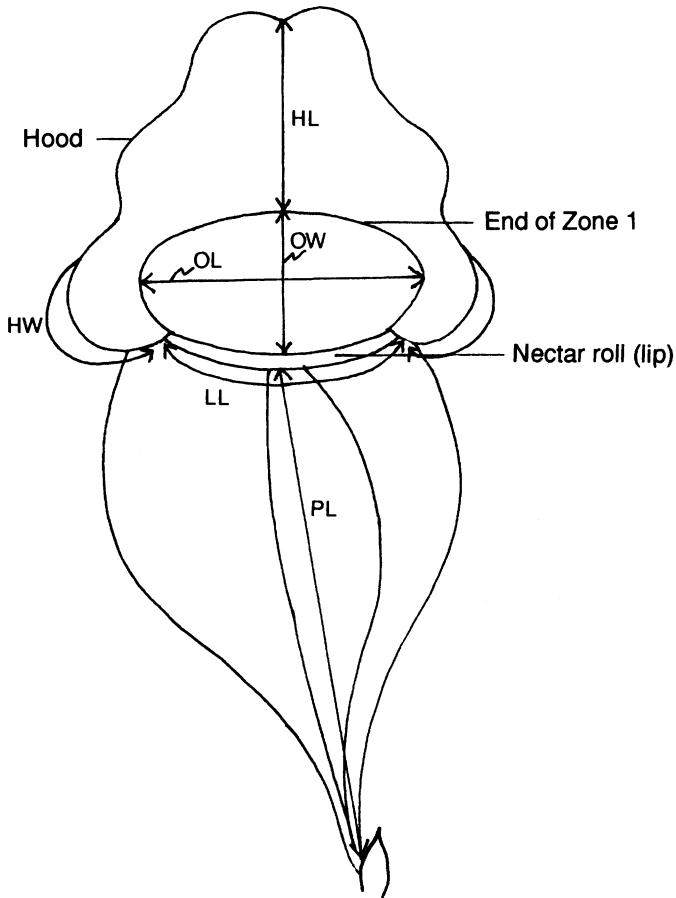


FIG. 1.—Diagram of morphological characteristics measured on 87 pitchers in a population of *Sarracenia purpurea*. Key to pitcher measurements: OL*, Opening length; OW*, Opening width; PL*, Pitcher length; HL*, Hood length; HW, Hood width; LL, Lip length. The hood is Zone 1 and contains downward-pointing hairs; the end of the hood is delimited by these hairs (Juniper *et al.*, 1989). All measurements were recorded in cm

*Measurements are linear distances. Other measures curve with the pitcher

widely investigated, there is little information regarding its role in prey attraction by carnivorous plants.

Sarracenia purpurea, the northern purple pitcher plant, has pigmented EFN guides on the surface of the pitcher which presumably lure insects toward the hood and nectar roll (lip) at the front of the pitcher (Juniper *et al.*, 1989) (Fig. 1). *Sarracenia purpurea* is visited by a wide variety of diurnal and nocturnal insects (Heard, 1998). Pitchers are visited most frequently during daylight with visitation much reduced at night (Newell and Nastase, 1995). Factors such as lower temperatures at night or greater quantities of nectar sugar available during the day may explain the visitation patterns. Our study addresses patterns in day/night yields of nectar sugar.

The quantity of available sugar, or caloric content, is an important factor influencing insect visitation patterns in that insects prefer plants or flowers that offer greater rewards (Devlin and Stephenson, 1985). In this study we define nectar rewards obtained by insect visitors in terms of sugar amount (*i.e.*, quantity of total carbohydrates collected by a paper wick) in the nectar.

Patterns of nectar sugar are influenced by several factors, including removal by insects (Wyatt and Shannon, 1986). Flowers exposed to insect visitors often have much lower sugar amounts than individuals whose nectar sources are experimentally protected and unavailable to insects (Davis, 1997). Pitchers of *S. purpurea* are visited by many insects which feed on the nectar (Newell and Nastase, 1998).

Environmental factors, such as relative humidity and temperature, also influence sugar amount (*e.g.*, Corbet *et al.*, 1979a; Kradolfer and Erhardt, 1995). Most studies have focused on the effects of environment on other nectar qualities, such as nectar secretion rates and concentration of various sugars in nectar (*e.g.*, Cruden *et al.*, 1983; Wyatt *et al.*, 1992). Sugar concentration refers to the amount of sugar per unit volume of nectar. Amount of sugar in nectar is independent of volume; any given amount of sugar may be present in a more or less concentrated solution.

Intraspecific variation in the morphology of pitcher plants is well documented (Newell and Nastase, 1998). Cresswell (1993) described correlations between prey capture and various measures of pitcher size. Newell and Nastase (1998) found that more potential prey visited plants with more red venation. Are these relationships determined by sugar amount?

The purpose of the present study was to analyze patterns of sugar amount in nectar from pitchers of *S. purpurea*. We addressed the following questions in our study: (1) Do pitchers present variable nectar rewards in terms of sugar amount throughout the day?, (2) Are sugar amounts lower when pitchers are exposed to insects?, (3) Do environmental factors affect sugar amount throughout the day and night? and (4) Do differences in pitcher size and degree of red coloration (*i.e.*, color rank) result in differential daily sugar rewards offered to insect visitors?

MATERIALS AND METHODS

We collected nectar samples from pitchers of *Sarracenia purpurea* plants located in the Forest Service Bog at the University of Notre Dame Environmental Research Center (UN-DERC) in northern Wisconsin (46°13'N, 89°32'E, 510 m elev.). We used healthy plants large enough to accommodate the wick-sampling technique and randomly assigned them to a bagged ($n = 29$) and nonbagged ($n = 58$) treatment. Bridal veil (mesh size 10×10 threads·cm⁻¹) was used to bag individual pitchers approximately 24 h before sampling. This technique prevented insects from removing nectar while having minimal effect on the microenvironment of the pitcher (Wyatt *et al.*, 1992). We obtained nectar samples from the youngest, fully developed pitcher on each plant, since it has been shown to produce the greatest amount of carbohydrates (Cipollini *et al.*, 1994). We repeatedly collected nectar samples from individual pitchers at 3 h intervals for 24 h, resulting in eight sampling periods per pitcher. Several pitchers (10–15) were sampled on each sampling day (24 h period), the number being determined by what could be accomplished within the 3 h interval between samples. Different pitchers were sampled each 24 h period so that an individual was sampled for only 24 h. A total of 87 pitchers, each on a different plant, was sampled between 19 July and 8 August 1995. Pitchers were not sampled during inclement weather and at least 36 h was required between sampling days to allow investigators to select plants for the following sampling day, measure the pitchers and allow bagged individuals to acclimate to the treatment. Sampling was initiated at a different hour for different pitchers to

avoid bias in sampling. In other words, sampling time was stratified, such that the first sample from a pitcher might fall at 0900 h, 1200 h, 1500 h, 1800 h, 2100 h, 2400 h, 0300 h or 0600 h. The first sample collected from each pitcher was assigned a value of 1 and each subsequent sample was assigned a value of 2–8 based on its chronological order. Hereafter we refer to this value as the sample rank.

We collected nectar using the wick-sampling technique outlined by McKenna and Thomson (1988) and modified by Cipollini *et al.* (1994). Triangular wicks were cut from Whatman Number 1 filter paper using a specialized insect-mounting paper punch (base 3 mm, height 10 mm). Two wicks were gently clipped to the inside of the lip or nectar roll of the pitcher with vinyl-coated paper clips for 30 min. Nectaries are more densely located along the surface of the lip (Juniper *et al.*, 1989). Each wick was then placed in a microcentrifuge tube and stored at -18 C until later laboratory analysis.

Sugar amount was measured in terms of the total quantity of carbohydrates collected by our paper wicks. We determined the total sugar content in each nectar sample (wick) using a colorimetric anthrone assay modified for microliter volumes (Cipollini *et al.*, 1994). Sugars from the dried wicks were redissolved by agitation in $500\ \mu\text{l}$ Milli-Q water (water purified with a Milli-Q[®] water purification system, Millipore Corp., Bedford, Mass.) for 1 min using a vortex mixer. Aliquots ($100\ \mu\text{l}$) of each sample (3 replicates of each), reagent blanks and calibrating standards (see below) were transferred to fresh microcentrifuge tubes and placed in an ice bath for 30 min. Two hundred μl of anthrone reagent (0.01 M anthrone, $\text{C}_{14}\text{H}_{10}\text{O}$ [Sigma Chemical Corporation] in 98% concentrated H_2SO_4) were added to the microcentrifuge tubes. We vortexed tubes for 15 s and allowed them to incubate at room temperature for 90 min. The absorbance of the samples was read at 620 nm using a Cambridge Model 750 microplate reader (Packard Instrument Co.). A series of calibrating sugar standards ranging from 10–120 $\mu\text{g}/\text{ml}$ was prepared and used in each assay. Standards contained equal parts of fructose and sucrose since the actual sugar composition of the nectar is not known (Cipollini *et al.*, 1994). Sugar amount measured by our assay is the amount of sugar present on $10.5\ \text{mm}^2$ (area of wick) of the pitcher lip at the time of collection, rather than the amount present on the entire pitcher.

We summed the sugar amounts measured from 0900 h to 1800 h to yield the daytime sugar amount for each pitcher. The sugar amounts measured from 2100 h to 0600 h were summed to yield the nighttime sugar amount. We tested the differences in the mean sugar amount during the day and night using a Wilcoxon matched-pairs signed ranks test. Bagged and nonbagged pitchers were analyzed separately by treatment and together as a single group. We compared the mean sugar amount collected from bagged and nonbagged pitchers during each sampling period, during the day, at night and over 24 h using Wilcoxon rank sum *W* tests. We summed the amount of sugar/wick on the pitchers during all 8 sampling periods to yield the daily (24 h) sugar amount.

At the beginning of each sampling period we measured air temperature, ground temperature (3 cm below the surface) and relative humidity near the pitcher. These measures, along with time of day and sample rank, were correlated with sugar amount using Kendall's rank correlations.

We recorded the following morphological measurements for each pitcher sampled to analyze intraspecific variation in daily sugar amount of pitchers within the same population (Fig. 1): (1) lip length (LL): the total length of the pitcher lip from its attachment on one side of the hood, following the curve of the lip, to its attachment on the opposite side; (2) pitcher height (PH): the linear distance from the lip to the attachment of the petiole to the stem; (3) hood height (HH): the linear distance from the top of the hood to the end of zone 1 (where the hairs on the inside surface of the pitcher stop); (4) hood width (HW):

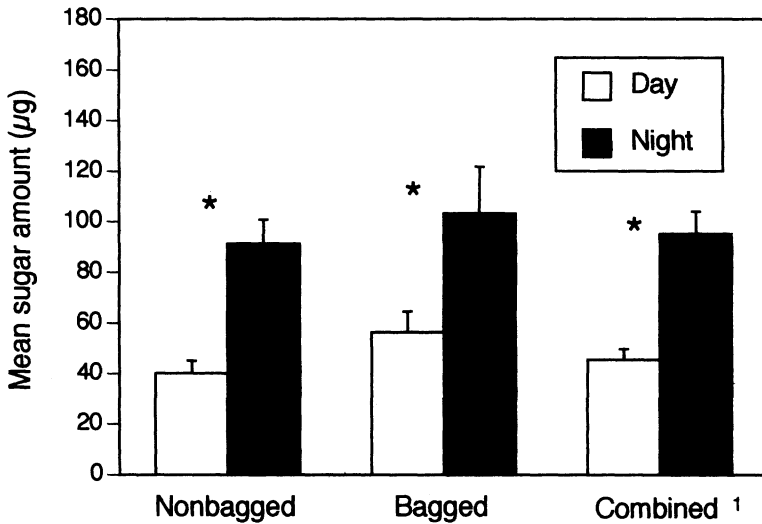


FIG. 2.—Mean sugar amount (μg total carbohydrates/wick) measured in nectar from nonbagged ($n = 58$) and bagged ($n = 29$) pitchers of *Sarracenia purpurea* during the day (0900 h to 1800 h) and night (2100 h to 0600 h). Error bars are $+1$ SE

¹Nonbagged and bagged pitchers were combined for analysis

*Wilcoxon matched-pairs signed ranks test comparing day and night sugar amounts, $P < 0.01$

the distance from one side of the hood to the opposite side at its greatest width, following the natural curve of the hood; (5) opening length (OL): the linear distance from one side of the pitcher opening to the opposite side at its greatest distance; opening width (OW): the perpendicular distance from the center of the lip to the back of the pitcher. Each pitcher was assigned a color rank from 1 to 5 according to the criteria outlined by Nastase *et al.* (1995), with 1 indicating pitchers having little or no red venation and appearing almost entirely green and 5 indicating pitchers with dark red, highly branched veins. We summed values of pitcher height and hood height to determine total height (TH) (Fig. 1). The opening area (OA) was calculated with values for opening width and length using the standard formula for the area of an oval (Nastase *et al.*, 1995). We analyzed the relationship between the above characteristics and daily (24 h) sugar amount using Kendall's rank correlations. In general, data did not meet the assumptions of parametric statistics and only nonparametric test results are reported. Parametric tests on both raw data and transformed data yielded similar results.

RESULTS

Both bagged and nonbagged pitchers presented significantly more nectar sugar at night than during the day (Fig. 2). Bagged pitchers consistently presented more nectar sugar than nonbagged pitchers during each sampling period; however, the differences were only significant at 1800 h (Fig. 3). At night sugar amount was the same for bagged and nonbagged pitchers (Wilcoxon rank sum $W = 1288.5$; $P = 0.91$). During the day sugar amount was higher on bagged pitchers, although the statistical analysis is not significant (Wilcoxon rank sum $W = 1485.5$; $P = 0.06$). During the day 29% of the nectar sugar was removed by

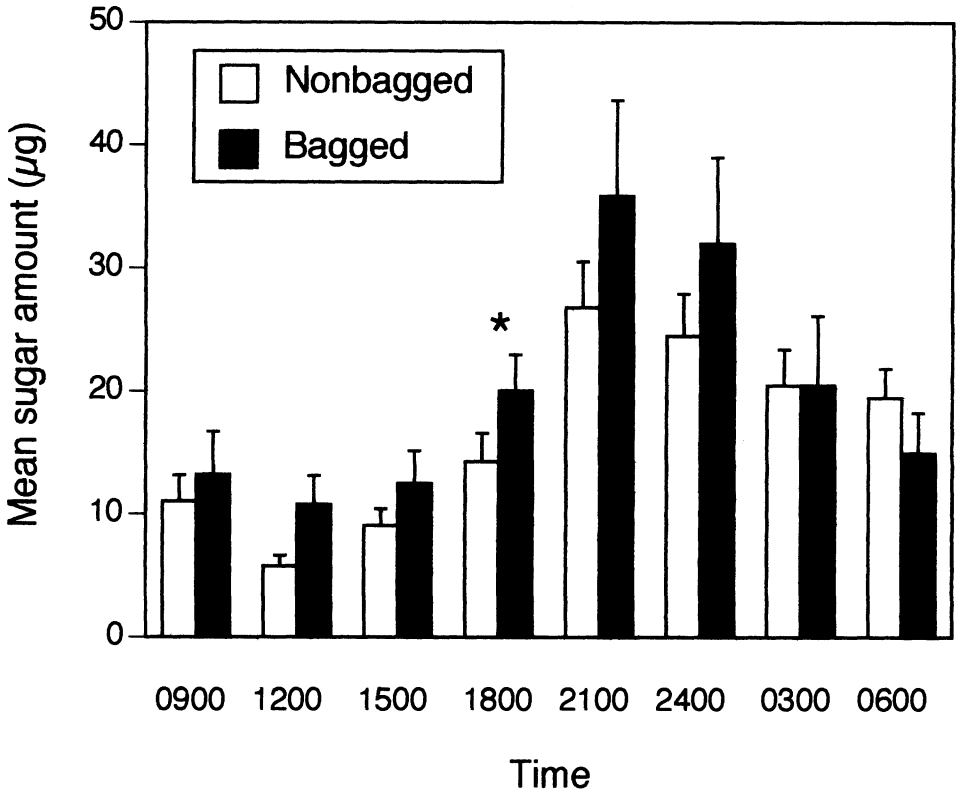


FIG. 3.—Mean sugar amount (μg total carbohydrates/wick) measured in nectar from nonbagged ($n = 58$) and bagged ($n = 29$) pitchers of *Sarracenia purpurea* during 8 consecutive sampling periods over a 24 h interval. Error bars are $+1$ SE

*Wilcoxon rank sum W tests, $P < 0.05$

visitors, in comparison to 16% removed at night. Over the 24 h sampling interval sugar amount was reduced by 18% on nonbagged pitchers.

Air temperature was negatively correlated ($P < 0.01$) with sugar amount on nonbagged pitchers and all pitchers combined, but not on bagged pitchers (Table 1). However, coefficient of determination (R^2) values were quite low, with air temperature explaining only 1–2% of the variation in sugar amount. Relative humidity and ground temperature were positively correlated ($P < 0.01$) with the amount of sugar on bagged and nonbagged pitchers analyzed separately and together (Table 1). Relative humidity explained 3% of variation in sugar amount on bagged pitchers and 7% of variation on nonbagged pitchers. Ground temperature explained 1–3% of variation in sugar amount on pitchers. Time of day showed a positive correlation ($P < 0.01$) with the amount of sugar on bagged pitchers and all pitchers combined, but not on nonbagged pitchers. However, it explained only 4% of variation in sugar amount on bagged pitchers and 1% of variation in nonbagged pitchers.

None of the nine pitcher characteristics was correlated with the daily sugar amount on the pitchers, analyzed separately by treatment or combined (Table 2).

TABLE 1.—Kendall's coefficients of rank correlation (τ) analyzing relationships between environmental factors and sugar amount measured in nectar from nonbagged and bagged pitchers at 3 h intervals over a 24 h period

	Nonbagged	Bagged	Combined ¹
Air temperature (C)	-0.10*	-0.05	-0.09*
Ground temperature (C)	0.11*	0.18*	0.13*
Relative humidity	0.19*	0.13*	0.17*
Time of day (h)	0.04	0.15*	0.08*
Sample rank (1-8) ²	-0.05	-0.06	-0.05

¹ Combined = Nonbagged and bagged pitchers were combined for analysis

² To avoid bias, sampling was initiated at a different time of day

* $P < 0.01$

DISCUSSION

We analyzed patterns of sugar amount in nectar from pitchers of *Sarracenia purpurea*. Greater quantities of nectar sugar were available at night than during the day on both bagged and nonbagged pitchers. The sugar amount peaked at 2100 h for both treatments. Similar patterns have been observed in other studies (Willson *et al.*, 1979; Willson and Bertin, 1979; Corbet *et al.*, 1979a). Large amounts of nectar sugar at night may be the result of increases in nectar secretion (Corbet, 1978; Willson *et al.*, 1979; Wyatt and Shannon, 1986), selective reabsorption during the day (Nepi *et al.*, 1996; Davis, 1997) or reduced insect visitation at night. We did not measure production rates nor reabsorption in this study and, therefore, are unable to attribute variation in sugar amount to these mechanisms. The high diurnal/low nocturnal visitation rates observed by Newell and Nastase (1995) are not sufficient in explaining the diel patterns in sugar amount documented in our study since pitchers with and without insects demonstrated similar patterns.

Another plausible explanation is that the patterns we observed in our study are related to environmental conditions. Sugar amount was positively related to relative humidity and negatively related to air temperature. Daytime temperature is higher and relative humidity is lower than at night. During the day the lips of the pitchers were dry and nectar appeared

TABLE 2.—Kendall's coefficients of rank correlation (τ) analyzing the relationship between morphological characteristics of individual pitchers and daily (24 h) sugar amount measured on nonbagged and bagged pitchers

	Nonbagged	Bagged	Combined ¹
Opening length (cm)	-0.09	0.05	-0.03
Opening width (cm)	0.06	0.16	0.09
Opening area (cm ²)	0.01	0.13	0.05
Pitcher length (cm)	-0.09	-0.04	-0.08
Hood length (cm)	0.00	0.04	0.03
Hood width (cm)	-0.02	-0.06	-0.03
Lip length (cm)	0.04	0.04	0.04
Total length (cm)	-0.08	-0.03	-0.07
Color rank (1-5)	0.16	-0.01	0.10

¹ Combined = Nonbagged and bagged pitchers were combined for analysis

* $P < 0.05$

scant, but at night the lips were covered with moisture from condensation. We suspect that high ambient temperatures and low relative humidity during the day may have evaporated the nectar resulting in an increase in concentration and possibly a crystallization of the sugar. However, any sugar crystals present were not large enough to be observed in the field. Pitchers of *S. purpurea* have an open morphology. Nectar-producing structures are not protected from evaporative effects and are susceptible to prevailing ambient conditions, such as wind, temperature and humidity (Corbet *et al.*, 1979b; Southwick *et al.*, 1981). Similar effects of environment on concentration of sugar have been observed in the nectar of many species (*e.g.*, Muraoka and Watanabe, 1994).

Such concentration effects could cause an underestimation in the sugar reward measured during some times of the day. Moistened wicks may be better able to collect nectar sugar from surfaces open to the environment, especially during hot dry periods. On the other hand, moistened wicks may be unable to absorb additional fluid. Trials of this technique would clarify whether moistening the wick would improve uptake of concentrated sugars. Nevertheless, our comparisons made between treatments are not affected.

The high sugar amounts of *S. purpurea* recorded at night do not coincide with the highest insect visitation rates, which occur during the day (Newell and Nastase, 1995). Insect visitation patterns may be mediated by other nectar characteristics, such as nectar volume or concentration of sugar per unit volume of nectar. Investigators studying bee and wasp visitation to flowers have described positive relationships between visitation and sugar concentration, in that peak visitation rates corresponded with periods of high concentration (39–50%) (Corbet, 1978; Southwick *et al.*, 1981; Wyatt and Shannon, 1986), because they can obtain maximum caloric rewards in terms of unit volume rather than per visit (Willson *et al.*, 1979). *Sarracenia purpurea* may be offering a more concentrated nectar during the day. During periods of high nectar sugar concentration and possible crystallization of sugar more sugar may be available to insects than our wicks. Diurnally active insects that are capable of regurgitating liquid onto viscous nectar can ingest large quantities of sugar. Both flies (Barth, 1991) and mosquitoes (Clements, 1992), common visitors to pitchers of *S. purpurea*, have been observed feeding on crystallized sugar in this manner in the laboratory. Volume of nectar is less likely to be an important factor influencing visitation patterns since pitchers have an open morphology and nectar, regardless of its quantity, is accessible to all insects.

During the day when insect activity is greater (Newell and Nastase, 1995), the sugar amount on the nonbagged pitchers was reduced (29%) relative to the bagged pitchers. There was a smaller difference (16%) in the amount of sugar measured on the two groups at night, when insect activity is less. Muraoka and Watanabe (1994) described similar patterns also attributing them to greater insect activity during the day. Sugar depletion in nonbagged flowers open to visitors has been commonly cited (Nepi *et al.*, 1996; Davis, 1997). Flowering plants receive potential benefits from visitors in the form of pollination, and greater insect activity should be expected to increase chances of being pollinated. For carnivorous plants, the benefits associated with nectar sugar production are quite different since they are measured in terms of potential prey and subsequent nutrients. Newell and Nastase (1998) observed low capture rates by pitchers, which coupled with large amounts of nectar removal by insects, suggests that this may impose considerable costs to the pitcher. It is not possible to calculate these costs using our data.

Other than condensation of dew at night, environmental factors, such as relative humidity and air and ground temperature, had little influence on the observed patterns of sugar amount. Despite the statistical significance of several relationships between relative humidity and temperature and sugar amount, they explain only 1–7% of the variation in sugar amount. Previous studies have described variable relationships between humidity and tem-

perature and sugar amount (Corbet *et al.*, 1979a; Jakobsen and Kristjánsson, 1994; Kradolfer and Erhardt, 1995). Many studies have noted significant relationships between relative humidity and temperature and concentration of sugar in nectar (Corbet *et al.*, 1979b; Bertsch, 1983). In addition, high relative humidity and higher temperatures can stimulate nectar production (Butler *et al.*, 1972; Wyatt *et al.*, 1992). Previous studies have not measured the relationship between ground temperature and nectar characteristics. Additional measurements of these variables (*i.e.*, nectar production and concentration) may shed light on environmental lability of pitcher nectar.

Although pitchers of *Sarracenia purpurea* demonstrate much variation in size and coloration, these differences are not related to variations in sugar amount. Pitcher characteristics may be related to other nectar traits, such as volume and sugar concentration, but it seems unlikely.

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