

## PREY ADDITION ALTERS NUTRIENT STOICHIOMETRY OF THE CARNIVOROUS PLANT *SARRACENIA PURPUREA*

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**Abstract.** The carnivorous pitcher plant *Sarracenia purpurea* receives nutrients from both captured prey and atmospheric deposition, making it a good subject for the study of ecological stoichiometry and nutrient limitation. We added prey in a manipulative field experiment and measured nutrient accumulation in pitcher-plant tissue and pitcher liquid, as well as changes in plant morphology, growth, and photosynthetic rate. Prey addition had no effect on traditional measures of nutrient limitation (leaf morphology, growth, or photosynthetic rate). However, stoichiometric measures of nutrient limitation were affected, as the concentration of both N and P in the leaf tissue increased with the addition of prey. Pitcher fluid pH and nitrate concentration did not vary among treatments, although dissolved oxygen levels decreased and ammonia levels increased with prey addition. Ratios of N:P, N:K, and K:P in pitcher-plant tissues suggest that prey additions shifted these carnivorous plants from P limitation under ambient conditions to N limitation with the addition of prey.

**Key words:** carnivorous plants; field experiment; K:P ratio; N:K ratio; N:P ratio; nitrogen; nutrient limitation; phosphorus; *Sarracenia purpurea*; stoichiometry.

### INTRODUCTION

Ecological analyses of relationships between essential nutrients and energy—*ecological stoichiometry* (Stern and Elser 2002)—can provide important insights into processes that control patterns of species distributions, abundances, and population dynamics. For example, if nutrient availability limits growth (Aerts and Chapin 2000), then ratios of nitrogen and phosphorus (N:P) (Koerselman and Meuleman 1996, Bedford et al. 1999) or nitrogen, phosphorus, and potassium (N:P:K) (Olde Venterink et al. 2002, 2003) in plant tissue can predict nutrient limitations of both individual plants and entire communities (Aerts and Chapin 2000). By these criteria, many European wetlands and North American bogs tend to be N limited, but other North American wetlands tend to be P limited (Bedford et al. 1999).

The purple pitcher plant *Sarracenia purpurea* L. (see Plate 1) is a model system for studying ecological stoichiometry because the production of carnivorous pitchers and flat photosynthetic leaves (phyllodes) is altered by nutrient inputs (Ellison and Gotelli 2002). Carnivorous plants grow commonly in nutrient-poor habitats such as ombrotrophic bogs (Givnish et al. 1984), and rely in whole or in part on captured prey to supply essential nutrients (Chapin and Pastor 1995). Growth and reproduction of most carnivorous plants are limited by available nitrogen (Ellison and Gotelli 2001) and

many species alter production or morphology of carnivorous organs in response to nutrient input (Knight and Frost 1991, Ellison and Gotelli 2002).

Because pitcher plants are sensitive to N:P input ratios, we expect them to respond differently to two different forms of nutrient input: captured prey and atmospheric deposition. Captured prey (mostly arthropods) include N, P, K, Ca, and other nutrients that potentially enhance plant growth, but cannot be used by the plant until they are released by decomposition and feeding activities of the specialized invertebrate community that inhabits *Sarracenia* pitchers (Heard 1994). Atmospheric deposition ( $\text{NO}_3$  and  $\text{NH}_4$ ) does not include other essential elements, but does provide a source of biologically active nitrogen that is immediately available for plant uptake (Ellison and Gotelli 2002).

In this study, we used a controlled field experiment to test for the effect of prey addition on the morphology, stoichiometry, and photosynthetic rates of *Sarracenia purpurea*. We hypothesized that pitcher plants would respond to additional prey by increasing leaf biomass, photosynthetic rate, and nutrient absorption. We further predicted that because of the difference in nutrient content between prey and atmospheric deposition, plant morphology (pitcher vs. phyllode production) would not be altered in prey-fed plants. Last, we compared N:P:K ratios in tissues of control and treatment plants to extend our understanding of pitcher-plant stoichiometry and to evaluate evidence for N, P, and K (co-)limitation in this species.

In agricultural systems, traditional measures of plant responses to nutrient additions include shifts in plant

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PLATE 1. In the carnivorous plant *Sarracenia purpurea*, the concentration of leaf-tissue nitrogen and phosphorus increases in response to experimental prey additions. Photo credit: N. J. Gotelli.

morphology, growth, biomass, or photosynthetic rate. However, these measures may not always be the best way to detect nutrient limitation in natural communities (Chapin et al. 1986). In this study, we have measured plant morphology, growth, biomass, and photosynthetic rate, as well as measures of tissue nutrient accumulation in order to document shifts in ecological stoichiometry that also indicate nutrient limitation (Sternier and Elser 2002).

#### MATERIALS AND METHODS

##### *Study species*

*Sarracenia purpurea* is a rosette-forming perennial plant that grows in sunny, nutrient-poor sphagnum bogs, seepage swamps, and the occasional poor fen throughout the eastern coastal plain, New England, and the upper mid-west of the United States, and from Atlantic Canada west to British Columbia (Ellison et al. 2004). Pitcher plants have weakly developed root systems (Juniper et al. 1989) and the bulk of their nutrients are obtained from insect prey attracted to the brightly colored pitchers and extrafloral nectaries (Chapin and Pastor 1995, Ellison and Gotelli 2001). The prey is trapped and drowns in the pitchers, and nutrients from the decomposing insects are absorbed by the leaf (Juniper et al. 1989). Unlike the other species of *Sarra-*

*cenia*, *S. purpurea* pitchers accumulate rainwater and an associated community of specialized invertebrates, along with protists and bacteria (Heard 1994). Captured prey is the basal resource for this food web, which shreds the prey and mineralizes the available nutrients (Heard 1994). Prey capture by *S. purpurea* is relatively inefficient: <1% of the potential prey that visit a pitcher are captured (Newell and Nastase 1998), and capture efficiency decreases within four weeks after a pitcher opens (Fish and Hall 1978). The total biomass of captured prey between pitchers is highly variable, but pitcher density does not generally affect capture rate (Cresswell 1991). The primary insect prey at our study sites are ants (Gotelli and Ellison 2002a) and flies (A. M. Ellison and N. J. Gotelli, *unpublished data*).

In New England, a new leaf (pitcher or phyllode) is produced every 10 to 14 days during the growing season; on average five leaves are produced annually (Fish and Hall 1978). Although some leaves persist into the subsequent growing season, they senesce over the course of the summer as new leaves are produced, resulting in a relatively constant number of pitchers per plant (Fish and Hall 1978).

##### *Experimental methods*

We experimentally manipulated prey levels in pitcher plants growing at Belvidere Bog, an 2-ha level bog

in Vermont, USA (44° N, 72° W), in order to determine the effect of prey addition on morphology, photosynthetic rate, water chemistry, and stoichiometry of *S. purpurea*. In May 2002 we haphazardly chose 200 non-flowering adult plants (rosettes  $\geq 10$  cm) in the open area of the bog. A distance of at least 50 cm separated all experimental plants. Each plant was randomly assigned to one of eight treatment levels ( $N = 25$  plants per treatment), corresponding to 0-7 frozen houseflies (mean dry mass = 1 mg; 103 mg N/g; 7.6 mg P/g; 9.2 mg K/g; 1.7 mg Ca/g; 1.4 mg Mg/g) fed twice weekly to each pitcher throughout the summer. Because house flies are heavier and have less chitin than most natural arthropod prey, these additions represented substantial increases over background levels of prey intake. Flies were added only to pitchers produced during the 2002 growing season; prey addition began when the first new pitchers were produced (24 June 2002) and continued until 12 September 2002. We added distilled water as necessary to maintain pitcher fluid at half of the leaf volume (5–10 mL). Pitchers on each plant were numbered sequentially in order of opening date (Leaf I, Leaf II, Leaf III, etc.) and each leaf was fed until they were harvested for analysis.

At approximately two-week intervals (10 and 29 July, 13 August, 2 and 15 September), all fed pitchers were harvested from each of five randomly chosen plants from each treatment group. Immediately before each harvest, dissolved oxygen content of the pitcher fluid (milligrams per liter and percentage saturation) of each leaf designated for that harvest was measured in situ using a YSI-58 dissolved oxygen meter (YSI instruments, Yellow Springs, Ohio, USA). Each pitcher was then cut off at the base; pitcher fluid was poured into sterile plastic tubes (50-mL centrifuge tubes) for subsequent analysis and the pitcher itself placed into a Ziploc plastic bag. All harvested material was kept cool and returned to the laboratory for processing within 4 h.

In the laboratory, the pitcher fluid was filtered using a Millipore Sterifil Aseptic system (Millipore Corporation, Billerica, Massachusetts, USA). The pH of the filtrate was measured with an Orion Model 290A portable pH/ISE meter (Thermo Electron Corporation, Waltham, Massachusetts, USA), and nitrogen (both  $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$ ) and phosphorus ( $\text{PO}_4\text{-P}$ ) concentrations were determined spectrophotometrically using standard methods (Bledzki and Ellison 1998, Clesceri et al. 1998). The length, mouth diameter, and maximum width ( $\pm 1$  mm) of each harvested pitcher or phyllode was measured, along with the width of its wing (keel); see Ellison and Gotelli (2002) for an illustration of these measurements. All leaves were dried at 70°C for 3–5 days, and individually weighed and ground for nutrient analysis at the University of Vermont Agricultural and Environmental Testing Laboratory (Burlington, Vermont, USA).

TABLE 1. Dissolved oxygen and  $\text{NH}_4\text{-N}$  in the fluid of Leaf I as a function of number of flies added to the pitcher.

No. flies added per week	Dissolved oxygen (mg/L)	$\text{NH}_4\text{-N}$ (mg/L)
0	$2.9 \pm 1.00$	$0.4 \pm 1.03$
2	$2.6 \pm 0.73$	$0.8 \pm 0.98$
4	$1.9 \pm 1.11$	$1.4 \pm 1.61$
6	$1.8 \pm 0.81$	$1.4 \pm 1.49$
8	$1.7 \pm 1.19$	$2.3 \pm 1.8$
10	$1.4 \pm 0.83$	$2.7 \pm 1.69$
12	$1.1 \pm 1.09$	$3.1 \pm 1.76$
14	$0.6 \pm 0.62$	$3.5 \pm 1.48$

Note: Values are means  $\pm$  SD;  $N = 25$  plants/treatment.

On 15 August 2002 we measured maximum photosynthetic rates of the Leaf I on two randomly selected plants from each treatment level. These plants were all harvested at the fourth harvest (2 September). Photosynthesis measurements were made in full sun, between 09:00 and 14:00 hours, using a LI-COR 6200 photosynthesis system (LI-COR, Lincoln, Nebraska, USA) and custom built 4-L chamber (Ellison and Gotelli 2002). During all measurements, ambient solar radiation exceeded the saturating photosynthetic photon flux density of *Sarracenia* ( $\text{PPFD} > 800 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ).

#### Statistical analyses

We used two-way analyses of variance (ANOVA) using S-Plus 6.1 (Insightful Corporation, Seattle, Washington, USA) to compare mean responses of Leaf I to different feeding treatments at the different harvest dates. Both numbers of flies added and harvest date were treated as random variables in this ANOVA, so the appropriate error term for these main effects in the ANOVA is the harvest  $\times$  treatment mean square, and the error term for the interaction term is the residual mean square (Gotelli and Ellison 2004). Observed responses of Leaves II and III to the treatments were qualitatively similar to those of Leaf I, but because some plants had fewer than three leaves, we illustrate and discuss only the results for Leaf I. As measurements of photosynthesis were conducted only once, these values were compared among treatment levels using a one-way, random-effects ANOVA. Variables were  $\log_{10}$  transformed as necessary to normalize variances and eliminate heteroscedasticity.

## RESULTS

### Characteristics of the pitcher fluid

With increasing number of flies fed to the pitchers, dissolved oxygen concentration in the pitcher fluid decreased ( $F_{7,21} = 9.89$ ,  $P < 0.001$ ; Table 1) and  $\text{NH}_4\text{-N}$  content increased ( $F_{7,28} = 9.51$ ,  $P < 0.001$ ; Table 1). Dissolved oxygen concentrations were similar across harvests early and late in the summer (2 mg/L), but decreased to 1.2 mg/L in midsummer at Harvest 3 ( $F_{3,21} = 10.8$ ,  $P = 0.03$ ).  $\text{NH}_4\text{-N}$  increased from an early season low of  $1.3 \pm 1.73$  mg/L to a midsummer peak

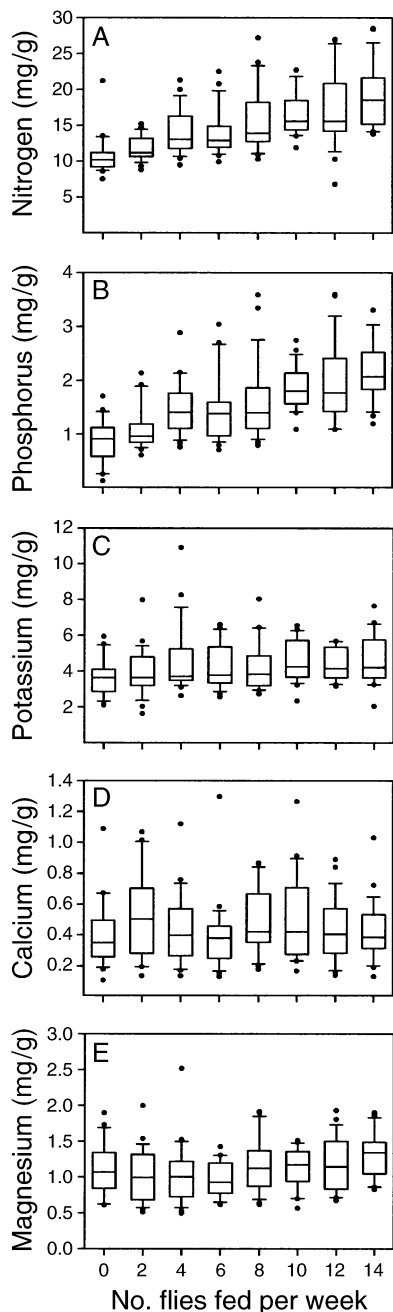


FIG. 1. Nutrient concentrations in pitchers fed varying numbers of flies. Data are for first leaves only;  $N = 25$  plants per treatment. Values are pooled across all five harvests. Box plots illustrate median (center horizontal line), upper and lower quartiles (edges of boxes), upper and lower deciles (ends of vertical lines) and individual values beyond the upper and lower deciles (solid circles).

of  $2.5 \pm 1.90$  mg/L ( $F_{4,28} = 4.60$ ,  $P = 0.006$ ), and then leveled off at  $2.1 \pm 1.80$  mg/L. Neither pH (grand mean =  $6.2 \pm 1.06$  [SD]),  $\text{NO}_3\text{-N}$  ( $0.16 \pm 0.39$  mg/L), nor  $\text{PO}_4\text{-P}$  ( $0.69 \pm 0.87$  mg/L) changed significantly with different numbers of flies added or varied significantly

over the course of the summer. There were no interactions between treatment and harvest date for any variable measured in the pitcher fluid.

#### Nutrient content of the pitcher tissues

Nitrogen (Fig. 1A), phosphorus (Fig. 1B), and potassium (Fig. 1C) concentrations in pitcher leaves all increased with increasing number of flies added (N:  $F_{7,28} = 15.19$ ,  $P < 0.001$ ; P:  $F_{7,28} = 13.14$ ,  $P < 0.001$ ; K:  $F_{7,28} = 4.34$ ,  $P = 0.002$ ). Magnesium varied across treatments ( $F_{7,28} = 4.61$ ,  $P = 0.002$ ), but not in a consistent direction (Fig. 1E). Neither N ( $F_{4,28} = 0.42$ ,  $P = 0.79$ ) nor P ( $F_{4,28} = 1.25$ ,  $P = 0.31$ ) in leaf tissue varied with harvest date, but K and Mg both decreased through the growing season (K:  $F_{4,28} = 65.59$ ,  $P < 0.001$ ; Mg:  $F_{4,28} = 16.52$ ,  $P < 0.001$ ). Calcium (Fig. 1D) did not vary among treatments ( $F_{7,28} = 1.76$ ,  $P = 0.13$ ), but increased significantly during the growing season ( $F_{4,28} = 17.82$ ,  $P < 0.001$ ). As with nutrients in pitcher fluid, there were no interactions between treatment and harvest date for any nutrient measured in the pitcher tissue.

The N:P ratio of the control plants was significantly higher than that of any of the fed plants ( $F_{7,28} = 5.98$ ,  $P < 0.001$ ; Table 2). However, the N:P ratios of the fed plants did not decrease significantly with the number of flies added ( $P > 0.05$ ; Tukey's HSD test). There was no significant difference in the N:P ratio among harvests ( $F_{4,28} = 2.35$ ,  $P = 0.08$ ), nor was there a significant interaction between treatment and harvest date ( $F_{28,155} = 1.12$ ,  $P = 0.32$ ). The N:K ratio of the plants fed 14 flies per week was significantly higher ( $P < 0.05$ , Tukey's HSD test) than either the control plants or plants in all the other treatments (overall  $F_{7,28} = 6.02$ ,  $P < 0.001$ ). N:K also differed among harvests ( $F_{4,28} = 16.37$ ,  $P < 0.001$ ); N:K at harvest 1 (N:K = 1.4) was  $\sim 25\%$  lower than N:K at the subsequent four harvests (N:K = 1.8).

#### Growth and morphology

There was no difference among treatments in the number of pitchers on the plants at each harvest date (grand mean =  $2.9 \pm 1.4$  [mean  $\pm$  SD] pitchers produced per plant;  $F_{4,28} = 0.515$ ,  $P = 0.815$ ). Because pitchers are produced throughout the growing season, it was not surprising that across treatments there were significantly more pitchers at later harvests than at earlier harvests ( $F_{4,28} = 35.510$ ,  $P < 0.01$ ). There was a significant interaction among treatments and harvests ( $F_{28,160} = 1.569$ ,  $P = 0.045$ ) but no consistent pattern of pitcher production across treatments. Individual morphological variables did not differ among treatment levels or through time (leaf length:  $161 \pm 38.4$  mm; leaf width:  $41 \pm 10.5$  mm; keel width:  $19 \pm 7.7$  mm; perpendicular mouth diameters:  $27 \pm 6.4$  and  $20 \pm 5.1$  mm [mean  $\pm$  SD]).

TABLE 2. Ratios of critical elements (N, P, K) in plant tissues of *Sarracenia purpurea* fed different numbers of flies.

No. flies added per week	Element ratios (mg/mg)		
	N:P	N:K	K:P
0	17.0 ± 3.05	3.1 ± 1.27	5.6 ± 4.26
2	11.8 ± 3.25	3.3 ± 1.22	3.8 ± 1.28
4	10.1 ± 2.28	3.3 ± 1.06	3.2 ± 0.92
6	10.5 ± 2.48	3.5 ± 1.31	3.3 ± 1.15
8	10.5 ± 2.08	3.9 ± 1.29	2.9 ± 0.98
10	9.1 ± 1.33	3.9 ± 1.22	2.5 ± 0.69
12	9.4 ± 2.62	3.9 ± 1.18	2.5 ± 0.71
14	9.1 ± 1.46	4.5 ± 1.85	2.3 ± 0.87
Threshold for limitation†	14.5	2.1	3.4

Notes: Values are means ± SD;  $N = 25$  plants/treatment. If the observed ratio exceeds the threshold for limitation, the results suggest limitation of the nutrient in the denominator. If the observed ratio falls below the threshold, the results suggest limitation of the nutrient in the numerator. See *Discussion* for additional details.

† Threshold ratios are from Olde Venterink et al. (2003).

### Photosynthetic rate

The average photosynthetic rate measured for plants in all treatments was  $3.1 \pm 1.2 \mu\text{mol CO}_2\text{-m}^{-2}\text{-s}^{-1}$  [mean ± SD]. We observed no significant difference in photosynthetic rate among treatments ( $F_{7,20} = 0.316$ ,  $P = 0.938$ ), and no relationship between tissue nitrogen content and photosynthetic rate ( $r = 0.17$ ,  $P = 0.4$ ).

### DISCUSSION

In wetlands, if plant tissue  $P < 1.0$  mg/g and  $N:P > 16$  mg/mg, phosphorus limitation is implied (Koerselman and Meuleman 1996). If plant tissue  $N < 20$  mg/g and  $N:P < 14$  mg/mg, then N limitation is suggested (Koerselman and Meuleman 1996). Olde Venterink et al. (2003) further assessed the importance of K limitation in wetland plants. They suggested K may be limiting if its concentration in plant tissue is  $< 8$  mg/g. Critical ratios indicating P or P+N limitation are  $N:P > 14.5$  mg/mg and  $K:P > 3.4$  mg/mg; for N limitation,  $N:P < 14.5$  mg/mg and  $N:K < 2.1$  mg/mg; and for K or K+N-limitation,  $N:K > 2.1$  mg/mg and  $K:P < 3.4$  mg/mg. Relatively high levels of nitrogen deposition occur in the northeastern United States (Ollinger et al. 1993), which may lead to a shift in nutrient limitation from N limitation to limitation either by P alone or jointly by N and P (Morris 1991).

In our study, prey additions significantly altered tissue nutrient content and stoichiometry of *Sarracenia purpurea* (Tables 1 and 2, Fig. 1). Traditional measures of nutrient limitation (plant morphology, biomass, growth, and photosynthesis) did not change with prey addition, although our measurements were restricted to within-season growth. The mean concentration of P in control (unfed) plants was  $< 1$  mg/g (Fig. 1B), and the corresponding N:P ratio of 17 mg/mg (Table 2) suggested that these plants were P limited. In contrast, the N:P ratios in all the other (fed) treatments were  $< 12$  mg/mg, suggesting N limitation (Table 2). Potassium concentrations in all treatments were well below the 8

mg/g level (Fig. 1C), indicating that K could also limit plant growth. However, N:K and K:P ratios (Table 2) suggest that K was not a significant limiting nutrient, given the low availability of N (Fig. 1A).

Collectively, these data suggest that prey additions shifted plants from being P limited under ambient conditions to being N limited (or N+K co-limited) when prey were added. Ratios of N:P, N:K, and K:P in plants receiving extra prey were strikingly different from the ratios observed in a complementary similar field experiment in which plants were fed soluble nutrients to pitchers (Ellison and Gotelli 2002); the latter was an experiment designed to mimic the impact of nutrient deposition from atmospheric sources on pitcher plants. In the current experiment, *S. purpurea* shifted from being relatively more P-limited with ambient prey inputs to being relatively more N limited when prey were added (Fig. 2). Although pitcher plants accumulated both N and P with prey additions (Fig. 1), P appears to have been taken up at a relatively faster rate, so the N:P ratio fell in the fed plants relative to the unfed controls (Table 2). In contrast, as soluble N (as  $\text{NH}_4\text{Cl}$ ) was added to pitchers in the Ellison and Gotelli (2002) study, *S. purpurea* shifted from being N limited to being P limited (Fig. 2). Changes in pitcher-plant stoichiometry appear to be controlled by both the quantity and form of nutrient inputs.

Prey addition had no obvious effects on plant morphology, photosynthetic rate, or growth within a single growing season. This finding also contrasts with results found when soluble nutrients were added to *S. purpurea* pitchers, which resulted in dramatic reductions of pitcher diameter, increases in keel size, and increases in photosynthetic rate (Ellison and Gotelli 2002), all of which occurred within a single growing season. This lack of a growth response when prey were added is consistent with results of Chapin and Pastor (1995), who also reported no effect of fertilizer or prey addition on aboveground plant biomass, number of leaves pro-

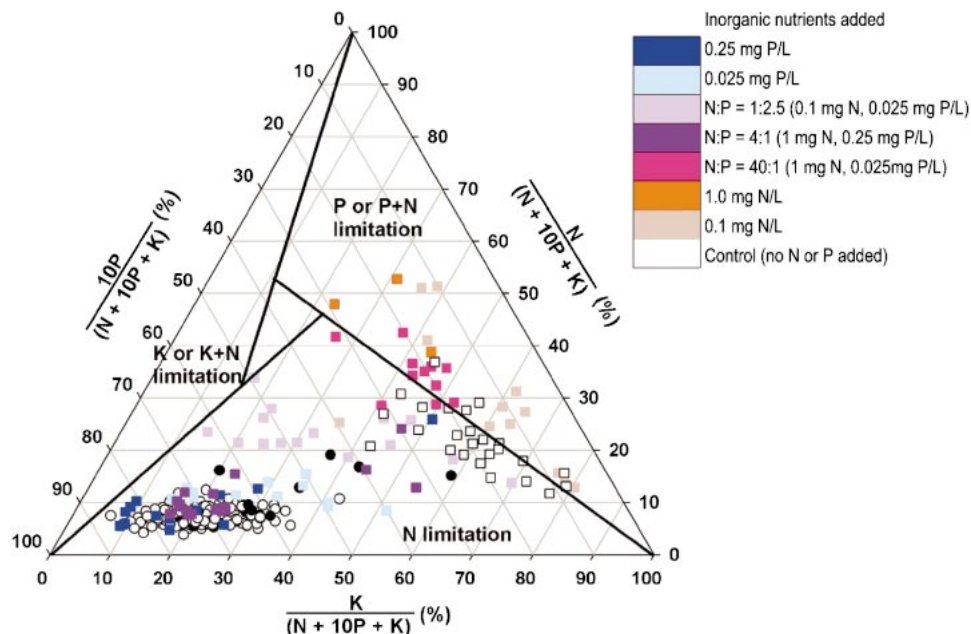


FIG. 2. Ternary plot illustrating N:P:K tissue ratios of *Sarracenia purpurea* fed flies (circles) or combinations of  $\text{NH}_4\text{NO}_3$  and  $\text{NaH}_2\text{PO}_4$  (squares). Circles are data from the prey-addition experiment (current study): solid circles, ambient prey controls; open circles, fly-addition treatments (2–14 flies/week). Colored squares are data from Ellison and Gotelli (2002); colors indicate N and P concentrations of nutrient solution added to the plant. Nutrient-limitation boundaries in the ternary plot are based on the criteria of Olde Venterink et al. (2003).

duced per season, or average leaf mass of *S. purpurea*. On the other hand, prey-addition experiments have increased plant biomass in several other carnivorous plants, including *Drosera* (Thum 1988), *Pinguicula* (Zamora et al. 1997), and *Sarracenia flava* (Christensen 1976).

We were somewhat surprised that the addition of prey did not increase pitcher photosynthetic rate, as it did when soluble N was added to pitchers (Ellison and Gotelli 2002). The cost–benefit model of Givnish et al. (1984) predicts that increased nutrients (i.e., prey) should increase the rate of photosynthesis because of the well-known relationship between photosynthetic capacity of leaves and nitrogen content (Field and Mooney 1986, Evans 1989). Pitcher plants readily store nutrients for growth and especially reproduction in subsequent years (Shreve 1906, Plummer and Kethley 1964, Schulze et al. 1997), and our results suggest that excess nutrients were being accumulated and stored for future growth or reproduction.

Prey captured by the pitcher is a resource not only for the plant, but also for the food web within the pitcher fluid (Heard 1994). Phosphate levels in the pitcher fluid did not differ by treatment level or harvest date, suggesting that the P mineralized by the food web was rapidly absorbed by pitcher tissue. In contrast, ammonium ( $\text{NH}_4\text{-N}$ ) concentration in the pitcher water increased with treatment rather than being entirely absorbed by plant tissue (Table 1), perhaps because N may be mineralized by the food web faster than it is

absorbed by the pitcher tissue. This contrasts with the findings of Bradshaw and Creelman (1984) who found no upper limit to the absorbance of  $\text{NH}_4$  excreted by *Wyeomyia smithii* and *Metriocnemus knabi*, two dipteran larvae that inhabit *S. purpurea* pitchers.

Recent papers that review studies of nutrient-addition experiments in wetlands have proposed that analysis of N:P:K ratios can be used to predict nutrient limitations at the community level (Koerselman and Meuleman 1996, Bedford et al. 1999, Olde Venterink et al. 2003). It is not clear yet whether these critical ratio limits can be applied to individual species (Güsewell 2004). Nevertheless, by some of these criteria, our unfed (control) plants were P limited, whereas plants that received additional prey were limited by N or N+K (Table 2). P limitation under ambient conditions is consistent with continental increases in N deposition from atmospheric sources (Morris 1991), and N deposition has been predicted to lead to the long-term decline of *S. purpurea* populations (Gotelli and Ellison 2002b). Continuing N deposition also may overwhelm any shifts in nutrient limitation caused by temporal changes in prey availability. The stoichiometry of *Sarracenia* reflects nutrient inputs from both prey and atmospheric sources, and continued monitoring may reveal the growing importance of atmospheric inputs.

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