

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

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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insect prey at our study sites are ants (Gotelli and Ellison 2002a) and flies (A. M. Ellison and N. J. Gotelli, *unpublished data*).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*



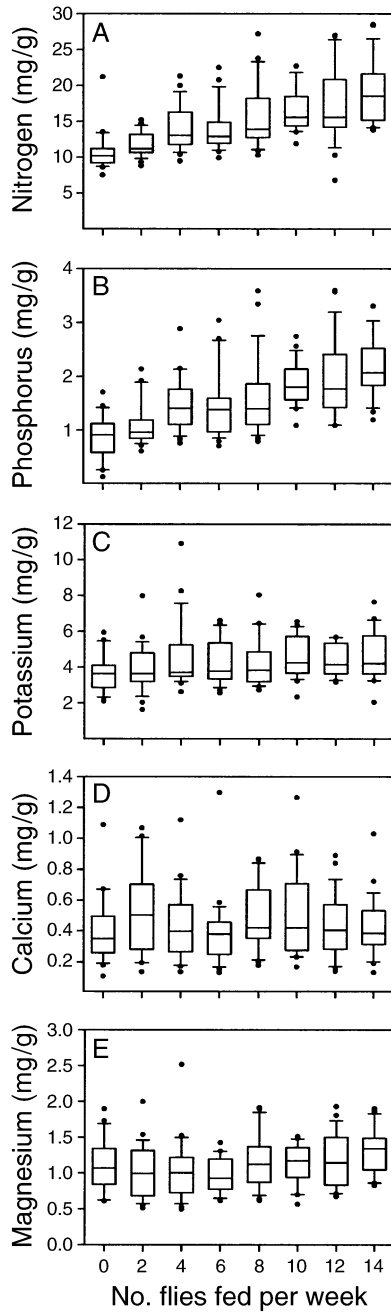


FIG. 1. Nutrient concentrations in pitchers fed varying numbers of flies. Data are for first leaves only;  $N = 25$  plants per treatment. Values are pooled across all five harvests. Box plots illustrate median (center horizontal line), upper and lower quartiles (edges of boxes), upper and lower deciles (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  $\text{PO}_4\text{-P}$  ( $0.69 \pm$

TABLE

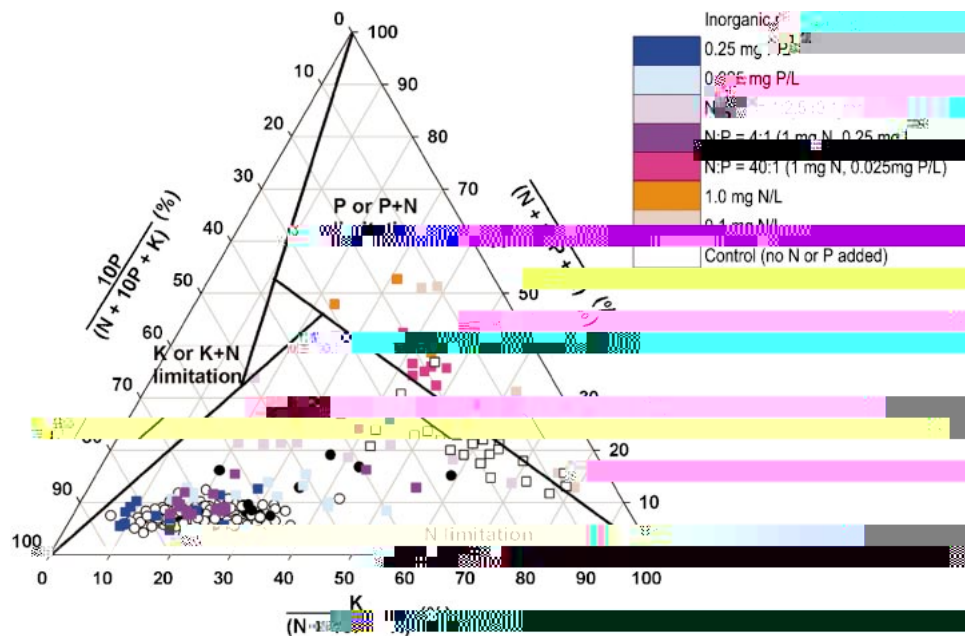


FIG. 2. Ternary plot illustrating N:P:K tissue ratios of *Sarracenia purpurea* fed flies (circles) or combinations of  $\text{NH}_4\text{NO}_3$  and  $\text{NaH}_2\text{PO}_4$  (squares). Circles are data from the prey-addition experiment (current study): solid circles, ambient prey controls; open circles, 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.

#### ACKNOWLEDGMENTS

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#### LITERATURE CITED

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## ERRATUM

In the recent paper by Amy E. Wakefield, Nicholas J. Gotelli, Sarah E. Wittman, and Aaron M. Ellison, “Prey addition alters nutrient stoichiometry of the carnivorous plant *Sarracenia purpurea*, *Ecology* **86**(7):1737–1743, there are errors in Fig. 2 and the associated text. In a review of the spreadsheet used to produce Fig. 2, the authors found that the values for %P and %K were tenfold too large (a result of converting from the mg/g illustrated in Fig. 1 to the percentage used in Fig. 2). As a result, the cloud of points illustrating the effects of adding insects to *S. purpurea* was placed incorrectly in Fig. 2. The original published figure also does not correctly reflect the N:P ratios given in Table 2.

The corrected figure only strengthens the conclusions of the paper. On page 1741, the published version says (underlining indicates words to be changed), “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).” The new figure suggests instead that “In the current experiment, *S. purpurea* shifted from being strongly P-limited to being limited by N or N+K when prey were added (Fig. 2).”

The corrected figure is available in ESA’s Electronic Data Archive: *Ecological Archives* E086-136.

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