Ecology, 89(4), 2008, pp. 898–904

Reports

LINKING THE BROWN AND GREEN: NUTRIENT TRANSFORMATION AND FATE IN THE *SARRACENIA* MICROECOSYSTEM

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Abstract. Linkages between detritus-based ("brown") food webs and producer-based ("green") food webs are critical components of ecosystem functionality, but these linkages are hard to study because it is difficult to measure release of nutrients by brown food webs and their subsequent uptake by plants. In a three-month greenhouse experiment, we examined how the detritus-based food web inhabiting rain-filled leaves of the pitcher plant *Sarracenia purpurea* affects nitrogen transformation and its subsequent uptake by the plant itself. We used isotopically enriched prey (detritus) and soluble inorganic nitrogen, and manipulated food web structure to determine whether the presence of a complete brown web influences uptake efficiency of nitrogen by the plant. Uptake efficiency of soluble inorganic nitrogen was greater than that of nitrogen derived from mineralized prey. Contrary to expectation, there was no effect of the presence in the food web of macroinvertebrates on uptake efficiency of either form of nitrogen. Further, uptake efficiency of prey-derived nitrogen did not differ significantly among *S. purpurea* and two congeneric species (*S. flava* and *S. alata*) that lack associated food webs. Although upper trophic levels of this brown food web actively process detritus, it is the activity of the microbial component of this web that ultimately determines nitrogen availability for *S. purpurea*.

Key words: carnivorous plants; detritus-based food web; nitrogen cycling; pitcher plants; producer-based food web; Sarracenia *spp.; stable isotopes.*

Introduction

Quantifying the contribution of detritus to food web structure and dynamics is an emerging frontier in ecological research (Moore et al. 2004). As detritus is processed through time—from large carcasses and particles to total mineralization—it is repeatedly transformed (Moore et al. 2004:596). Each transformation of detritus provides a point at which nutrients and energy flow out of detrital food webs and into surrounding ecosystems. It is particularly important to quantify which portions of a detritus-based ("brown") food web transform which portions of available detritus, and how the mineralized fractions are taken up by primary producers that are at the base of producer-based ("green") food webs (Ingham et al. 1985, Cole 1999, Setälä and Huhta 2001, Moore et al. 2004). However, most detritus-based food webs are in the soil. The fact that such brown food webs are poorly characterized and nutrient transfers in soil ecosystems are difficult to study has presented significant challenges for understanding how nutrients flow between brown and green food webs.

The detritus-based food web that inhabits the water-filled leaves of the northern pitcher plant, *Sarracenia purpurea*, is an alternative model system for studying direct linkages between brown and green food webs (Fig. 1). This aquatic detritus-based web is entirely above ground; it occurs in easily manipulated, replicate pitchers; and it has been studied and documented by zoologists and ecologists for many decades (Addicott 1974, Fish and Beaver 1978, Heard 1994, Cochran-Stafira and von Ende 1998, Miller et al. 2002, Ellison et al. 2003). Except for generalist protozoa and bacteria (Hepburn and St. John 1927, Cochran-Stafira and von Ende 1998, Whitman et al. 2005, Peterson et al., *in press*), all of the constituents of this five-trophic-level food web are obligate inhabitants of *S. purpurea* pitchers. Heard (1994) described the core elements of this system as a processing-chain commensalism: detritus → *Metriocnemus knabi* → particulate organic matter → bacteria → *Wyeomyia smithii*. Because the plant provides habitat and detritus (as captured prey) for the food web, which in turn provides nutrients mineralized from the detritus for the plant, the food web and the plant have long been considered to be obligate mutualists (Bradshaw and Creelman 1984). This mutualism is fragile, however, because increased rates of atmospheric nitrogen deposition lead to decreased production of carnivorous pitchers and consequently reduce habitat availability for the food web (Ellison and Gotelli 2002).

Here, we report the results of a three-month greenhouse experiment in which we quantified the relative contributions of arthropod prey and soluble

Manuscript received 13 August 2007; revised 21 November 2007; accepted 27 November 2007. Corresponding Editor: D. R. Strong.
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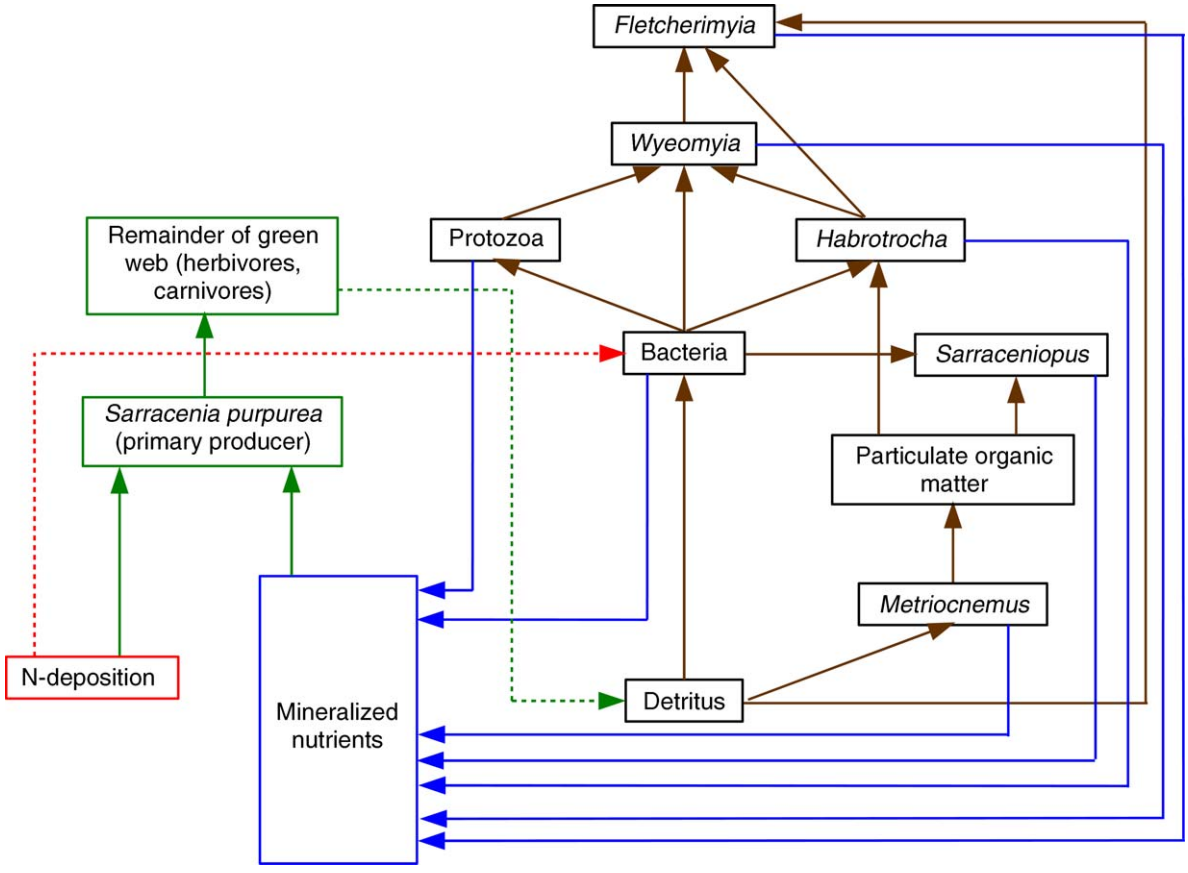

FIG. 1. The generalized *Sarracenia purpurea* microecosystem, illustrating linkages between the detritus-based food web that forms in the plant's rainwater-filled pitchers and plant productivity. Detritus enters the food web as arthropod prey captured by the plant. These carcasses are decomposed directly by bacteria or are shredded by both midge (*Metriocnemus knabi*) and flesh fly (*Fletcherimyia fletcheri*) larvae into particulate organic matter (POM), which in turn is consumed by bacteria, protozoa, and rotifers (*Habrotrocha rosa*). Mites (*Sarraceniopus gibsoni*) are primarily bacteriovores (Fashing 2005), but we have also observed them feeding on POM. The top predators (larvae of the mosquito *Wyeomyia smithii* and the sarcophagid fly *F. fletcheri*) feed omnivorously on bacteria, protozoa, rotifers (Addicott 1974, Heard 1994), and in the case of *F. fletcheri*, cannibalistically on other *F. fletcheri* (Forsyth and Robertson 1975) and on first- and second-instar *W. smithii* (L. A. Bledzki and A. M. Ellison, *personal observation*). All members of this brown (detritus-based) web excrete soluble nutrients (blue lines) that can be taken up by the plant itself (green line). Atmospheric deposition contributes additional soluble nutrients directly into pitchers (green line); some of these also may enter the detritus-based food web (red dotted line). Root uptake of nutrients by *Sarracenia purpurea* accounts for <2% of its overall nutrient budget (Butler and Ellison 2007). Plants themselves are at the base of a green (producer-based) web that includes ants, noctuid and tortricid moths (e.g., Atwater et al. 2006), small amphibians (e.g., Butler et al. 2005), and mammals; some of the members of this green web end up as prey in *Sarracenia*'s pitchers and reenter the brown web.

forms of nitrogen to the nutrient budget of *Sarracenia*, the primary producer at the base of the linked green food web (Fig. 1). We used isotopically enriched prey and soluble forms of nitrogen to assess the influence of the food web on nutrient acquisition by the plant. Our initial hypothesis was that the presence of a complete detritus-based food web in a *Sarracenia* pitcher would enhance the uptake efficiency of prey-derived N by the plant. We tested three predictions of this hypothesis: (1) nutrient uptake efficiency by the plant would differ for soluble inorganic nitrogen vs. prey-derived nitrogen; (2) the presence of higher trophic levels in the food web would increase uptake of prey-derived nitrogen but would have little effect on uptake of inorganic nitrogen; and (3) two other species of *Sarracenia* that do not harbor complex detritus-based food webs in their pitchers would be less efficient than *S. purpurea* in their uptake and translocation of prey-derived N. The surprising results of this study provide new insights into linkages between brown and green food webs.

METHODS

Study species

Sarracenia purpurea is a long-lived (≥50 years) carnivorous perennial plant that grows in bogs, seepage swamps, and fens throughout the eastern United States and across Canada (Schnell 2002). In northern bogs, pitchers are produced every two weeks; 5–10 pitchers are produced throughout each growing season (Fish and

Hall 1978). These pitchers fill with rainwater and a detritus-based food web (Fig. 1) develops within each pitcher within days of its opening (Fish and Hall 1978, Ellison et al. 2003). Although *S. purpurea* can produce some digestive enzymes, including proteases, phosphatases, RNases, and nucleases (Gallie and Chang 1997), it does not produce chitinases (Gallie and Chang 1997), and instead relies on the food web to shred the prey and initiate the decomposition and mineralization of captured prey. The excretory products of the food web, along with respired carbon dioxide, are taken up by the plant, which in turn captures prey for the food web, regulates ion concentration, and oxygenates the water in which the food web resides (Bradshaw and Creelman 1984, Joel and Gepstein 1985, Juniper et al. 1989, Meir et al. 1991).

We also contrasted uptake of nitrogen derived from prey by *S. purpurea* with uptake of nitrogen by two congeneric species, *S. alata* and *S. flava*. These latter two species are native to southeastern North America; like most of the eight other *Sarracenia* species, their pitchers are covered by a reflexed "hood" and do not fill with rainwater. Although bacteria, rotifers, and mites have been found in the pitchers of *S. alata* and *S. flava*, (Plummer and Jackson 1963, Baldwin and Menhinick 2000; R. F. C. Naczi, *unpublished data*), these pitcher plants rely almost entirely on endogenous digestive enzymes to break down and mineralize captured prey (Hepburn et al. 1927). In addition to having much taller pitchers than *S. purpurea*, *S. alata* and *S. flava* also have well-developed rhizomes and much larger root systems than *S. purpurea* (average total plant dry mass of our experimental plants was 0.91, 1.87, and 2.47 g, and the average ratio of belowground biomass [roots + rhizomes]: aboveground biomass ratio was 0.18, 0.71, and 0.71 for *S. purpurea, S. flava,* and *S. alata*, respectively).

Experimental design

We conducted this experiment in the greenhouse to control for natural food web development and prey capture in pitchers, to avoid overharvesting natural *Sarracenia* populations, and to minimize environmental differences among these three species that occur in different geographic regions. We added either unlabeled or ^{15}N-enriched forms of *Drosophila melanogaster* (as prey) and NH_4NO_3 (as soluble inorganic nitrogen) to assess the uptake of nitrogen from natural sources (prey) and from atmospheric deposition (soluble N). The C:N ratio of *D. melanogaster* is 4.71, somewhat larger than the C:N ratio of ants (3.38), the most common arthropod prey of *S. purpurea*. Soluble nitrogen derived from anthropogenic activities is an increasingly important component of the plant's nitrogen budget (Gotelli and Ellison 2002).

Forty-eight six-year-old, seed-grown *S. purpurea* plants were randomly assigned to one of four feeding treatments: (1) ^{15}N-NH_4NO_3; (2) ^{15}N-NH_4NO_3 plus unlabeled *D. melanogaster* (^{15}N-NH_4NO_3 + prey); (3) ^{15}N-*D. melanogaster* plus unlabeled NH_4NO_3 (^{15}N-prey + NH_4NO_3); and (4) ^{15}N-*D. melanogaster* (^{15}N-prey). ^{15}N-labeled $^{15}NH_4{}^{15}NO_3$ was enriched to 5 atom% ^{15}N (Isotec, Miamisburg, Ohio, USA), whereas *Drosophila* was enriched to 2.56 atom% ^{15}N by rearing larvae on 3 g of standard *Drosophila* medium (Carolina Biological Supply Company, Burlington, North Carolina, USA) to which 3 mg of 98 atom% ^{15}N L-glutamic acid and 2 mg of 98 atom% ^{15}N-glycine (Cambridge Isotope Laboratories, Andover, Massachusetts, USA) were added in 7.2 mL of tap water. Unlabeled flies were reared in a similar way except that unlabeled L-glutamic acid and glycine were added to the *Drosophila* medium.

The first four pitchers that opened on each plant were fed once each week with the appropriate prey and/or NH_4NO_3 combination. We monitored pitcher production throughout the experiment and began feeding a particular pitcher once it had fully opened and hardened. Each week, pitchers fed only NH_4NO_3 received a small aliquot (0.1–0.8 mL, depending on pitcher volume) of 100 ppm nitrogen (mg N/L) and were topped off to two-thirds the pitcher volume with distilled–deionized water (dd-H_2O); this resulted in a pitcher-water nitrogen concentration of 20 mg N/L. Over the course of the experiment, these *S. purpurea* plants received an average of 1.32 mg of NH_4NO_3-N (range: 0.54–2.68 mg of N). Pitchers fed only fruit flies were given 15 flies each week and were filled to two-thirds the pitcher volume with dd-H_2O. These plants received on average 9.5 mg of fly-N (range: 5.5–11.1 mg of fly-N) over the course of the three-month experiment. Pitchers fed both NH_4NO_3 and flies received the same doses as above, and were filled to two-thirds of the pitcher volume with dd-H_2O. The quantities of NH_4NO_3 and prey added to pitchers are comparable to the amount of nitrogen deposited in rainwater or available from captured prey (Chapin and Pastor 1995, Ellison and Gotelli 2002, Gotelli and Ellison 2002).

We assembled complete food webs in one-half of the plants, randomly chosen within each treatment group ($N = 6$ plants/treatment). These food webs consisted of 0.2 mL of field-collected, filtered (250-μm mesh) pitcher water (containing bacteria, protozoa, rotifers, and mites), 10 second-instar *Metriocnemus* larvae, 10 third-instar *Wyeomyia* larvae, and one second-instar *Fletcherimyia* larva. Pitchers were restocked with 10 third-instar *Wyeomyia* larvae halfway through the experiment to replace emerging adults; the other dipterans persisted as larvae throughout the experiment. The remaining plants in each treatment received food webs lacking larvae of the three dipterans. They were seeded with only bacteria and small protozoa by adding 0.2 mL of field-collected pitcher water filtered through a finer (6-μm) mesh. After the food webs were assembled, all pitchers were covered with fine nylon mesh to minimize capture of additional prey that occasionally wandered into the screened greenhouse.

To compare assimilation and subsequent translocation of prey-derived nitrogen by *S. purpurea* with other *Sarracenia* species, we applied the ^{15}N-prey treatment to four six-year-old seed-grown *S. alata* and four six-year-old seed-grown *S. flava* plants. Seed sources and growth techniques are described in detail in Ellison (2001). These two species received an average of 8.7 mg of prey-derived nitrogen (range: 6.4–10.0 mg of prey-N) over the three months. Pitchers of *S. alata* and *S. flava* were not filled with dd-H_2O, nor was the NH_4NO_3 treatment applied to them, as these species do not naturally collect water in their pitchers. All plants were grown in milled sphagnum (*Sphagnum magellanicum* Brid.) in $10 \times 10 \times 10$ cm plastic pots. Pots were saturated at least twice each week with dd-H_2O.

Measuring nitrogen uptake efficiency

Plants were harvested in mid-September after three months of feeding. Pitchers were separated from roots and rhizomes and thoroughly washed in tap water, followed by several rinses in dd-H_2O. Plant parts were dried for 48 hours at 65°C, weighed, and ground to a powder using a Wig-L-Bug grinder (Bratt Technologies, East Orange, New Jersey, USA). Subsamples were then weighed into 8×5 mm tin capsules (Elemental Microanalysis, Mason, Ohio, USA) and analyzed for total nitrogen and ^{15}N abundance at Yale University on a Finnigan DELTAplus Advantage continuous flow isotope ratio mass spectrometer and element analyzer (Thermo Scientific, Waltham, Massachusetts, USA). We also harvested three unlabeled control plants to provide baseline ^{15}N values in *Sarracenia* pitchers. To ensure that prey-derived nitrogen had in fact moved through the food web, we also dried and weighed all *Fletcherimyia* larvae at the end of the experiment, ground them individually, and analyzed them for ^{15}N abundance (*Fletcherimyia* larvae in the ^{15}N-NH_4NO_3 treatment were not measured because they had crawled out of their pitchers by the end of the experiment).

The uptake efficiency of labeled nitrogen was determined relative to unlabeled control plants as $100 \times (g\ ^{15}N_{plant}/g\ ^{15}N_{fed})$, where g $^{15}N_{plant}$ and g $^{15}N_{fed}$ refer to the total grams of ^{15}N recovered within the plant and the total grams of ^{15}N supplied to the plant, respectively. Uptake efficiency of *S. purpurea* was analyzed as a two-way, fixed-factor ANOVA (SAS version 9.1; SAS Institute 2002) with presence or absence of the food web and N-addition treatment as the two factors. The comparison of assimilation and translocation of prey-N by *S. purpurea* and the other two *Sarracenia* species was analyzed separately as a one-way ANOVA with species as a fixed effect. After finding no significant food web effects for *S. purpurea* (see *Results and discussion*), data for *S. purpurea* with and without food webs were pooled to compare nitrogen assimilation and translocation among the three species. Data were log-transformed to meet normality assumptions when necessary.

Results and Discussion

The accumulation of both soluble and prey-derived ^{15}N in tissues of the top predator *Fletcherimyia* confirms that both forms of nitrogen were transferred through the food web. *Fletcherimyia* larvae in plants fed with ^{15}N-prey were enriched to 1.52 ± 0.159 (mean $\pm$ SD) atom% ^{15}N and were significantly ($P < 0.0001$) more enriched than larvae in plants fed ^{15}N-NH_4NO_3 with unlabeled prey (0.40 ± 0.014 atom% ^{15}N). The latter value was slightly, but not significantly, higher than larvae in plants that were supplied with unlabeled *Drosophila* prey (measured in a separate experiment: 0.37 ± 0.0004 atom% ^{15}N; J. L Butler and A. M. Ellison, *unpublished data*). Because *Fletcherimyia* feeds omnivorously on carcasses, bacteria, rotifers, and small mosquito larvae (Fig. 1), the observed levels of enrichment of *Fletcherimyia* larvae in the different treatments suggest that NH_4NO_3 most likely entered the food web through the bacteria. In contrast, prey-derived nitrogen probably entered the food web through direct detritivory by these dipteran larvae.

The presence of dipteran larvae in the *S. purpurea* food web had no significant influence on the uptake efficiency of either form of nitrogen ($P = 0.358$; Fig. 2). However, the form in which nitrogen was provided significantly affected uptake efficiency of ^{15}N by *S. purpurea* ($P < 0.0001$; Fig. 2): pitchers assimilated a greater proportion of the available ^{15}N-NH_4NO_3 (mean = 67%) than the ^{15}N-prey (mean = 43%); this was evident when both N forms were available simultaneously.

Sarracenia purpurea depends largely on its food web to break down prey whereas *S. alata* and *S. flava* depend primarily on endogenously produced digestive enzymes. Nonetheless, these three species did not differ significantly in their uptake efficiency of nitrogen supplied from prey alone ($P = 0.959$); all three *Sarracenia* species assimilated between 40% and 50% of the available ^{15}N-prey (Fig. 2). The uptake efficiency of $^{15}NH_4{}^{15}NO_3$ by *S. purpurea* was similar to that reported by Butler and Ellison (2007) in an experiment examining nitrogen storage and remobilization by *S. purpurea*. Hanslin and Karlsson (1996) reported similar results for the uptake efficiency of ^{15}N-enriched *Drosophila* by three species of *Pinguicula* and one species of *Drosera*, all of which lack associated food webs.

Although *S. purpurea* plants acquired a greater *proportion* of the ^{15}N-NH_4NO_3 supplied to them, the acquired ^{15}N from prey represented a much greater *total portion* of the total plant N pool ($P < 0.0001$; Fig. 3). In both food web treatments ^{15}N-prey represented 0.35–0.48 mg of ^{15}N/mg of the nitrogen pool in *S. purpurea* plants, whereas ^{15}N-NH_4NO_3, represented only 0.07–0.15 mg (Fig. 3). *Sarracenia purpurea* pitchers in all treatments receiving prey (whether enriched or not) had significantly higher total nitrogen concentrations (1.10–1.36%; $P = 0.007$) than those plants receiving just ^{15}N-NH_4NO_3 (mean = 0.95%; Table 1). Wakefield et al. (2005) obtained a similar result in a field experiment in

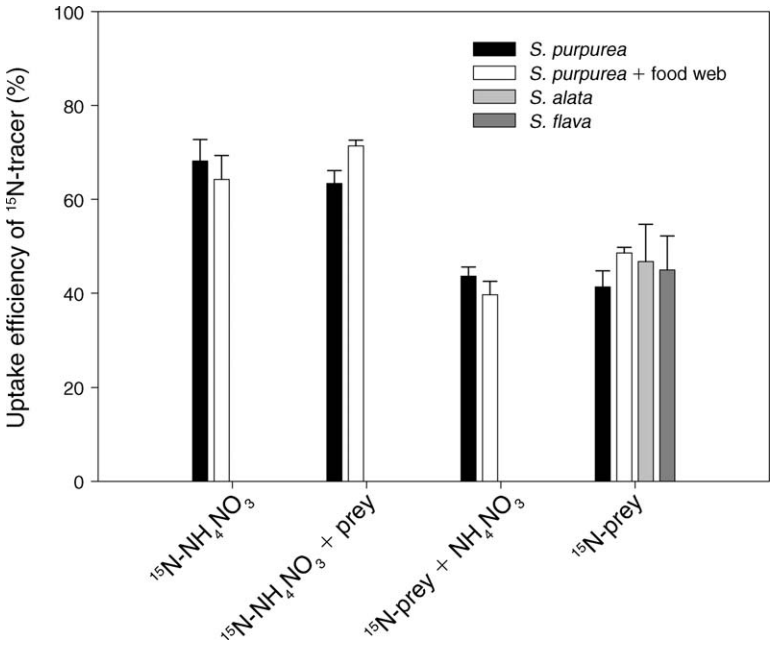

FIG. 2. Uptake efficiency of ^{15}N fed to *S. purpurea* as ^{15}N-NH_4NO_3 and/or ^{15}N-prey with and without food webs in *S. purpurea*, and of ^{15}N-prey in *S. alata* and *S. flava*. Bars are means, and error bars indicate one standard error of the mean from six replicate *S. purpurea* plants and four *S. alata* and *S. flava* plants. Within *Sarracenia purpurea*, the presence of the food web had no significant effect on uptake efficiency ($P = 0.358$), but the form of nitrogen fed to the plants did ($P < 0.001$). There was no significant feeding treatment × food web interaction ($P = 0.091$), nor did the three *Sarracenia* species differ in uptake efficiency when fed ^{15}N-*Drosophila* ($P = 0.959$).

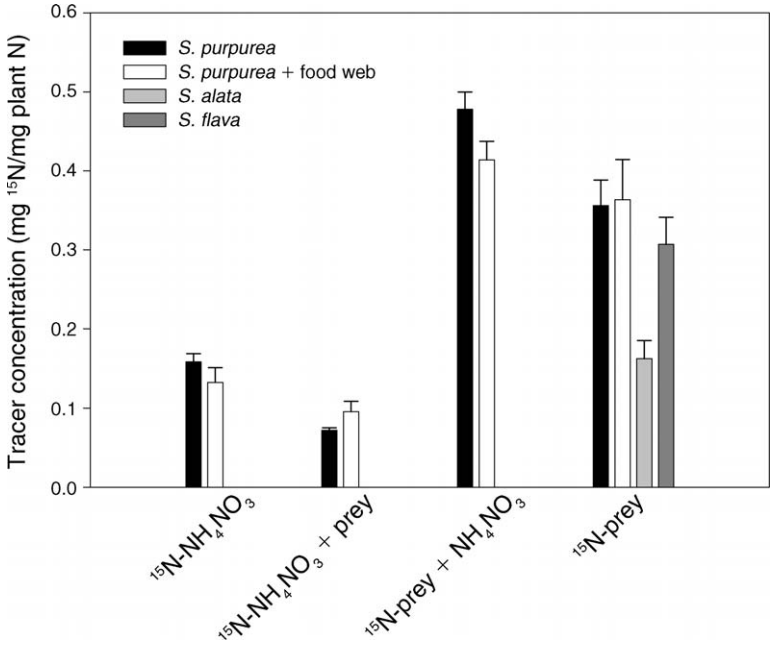

FIG. 3. Concentration of ^{15}N-tracer across all treatments for *Sarracenia purpurea* plants with and without food webs and for the ^{15}N-prey treatment for *S. alata* and *S. flava*. Bars are means, and error bars indicate one standard error of the mean; sample sizes are as in Fig. 2. For *S. purpurea*, the presence of the food web had no significant effect on concentration of ^{15}N tracer ($P = 0.421$), nor was there food web × N-feeding treatment interaction ($P = 0.281$). The form of N fed had a significant effect ($P < 0.001$) on ^{15}N concentration in *S. purpurea* pitchers, and ^{15}N concentration differed among the three *Sarracenia* species fed only ^{15}N-prey ($P = 0.048$).

TABLE 1. Nitrogen concentration (%) in living pitchers across all treatments and three *Sarracenia* species.

Treatment†	N concentration in living pitchers (%)			
	S. purpurea without food web	*S. purpurea* with food web‡	*S. alata*	*S. flava*
^{15}N-NH_4NO_3	0.92 (0.07)	0.98 (0.02)	ND	ND
^{15}N- NH_4NO_3 + prey	1.30 (0.05)	1.27 (0.07)	ND	ND
^{15}N-prey§	1.32 (0.14)	1.10 (0.09)	1.04 (0.08)	0.75 (0.03)
^{15}N-prey + NH_4NO_3	1.36 (0.13)	1.17 (0.14)	ND	ND

Notes: Values are means (with standard errors in parentheses) for six replicate plants for *S. purpurea* and four plants for *S. alata* and *S. flava*. ND indicates no data (treatment not applied).

† Significant effect ($P = 0.007$) of form-of-nitrogen-added on N concentration in *S. purpurea*.

‡ No significant effect ($P = 0.168$) of food web alone, and no significant food web × form-of-nitrogen-added interaction ($P = 0.474$) on N concentration in *S. purpurea*.

§ Concentration of nitrogen was significantly higher ($P = 0.009$) in *S. purpurea* and *S. alata* than in *S. flava* that were fed ^{15}N-enriched *Drosophila melanogaster*.

which *S. purpurea* was fed excess prey. Thus, although plants receiving both prey and ^{15}N-NH_4NO_3 assimilated a similarly large proportion of available ^{15}N-NH_4NO_3 as did plants receiving only ^{15}N-NH_4NO_3 (Fig. 2), the additional nitrogen derived from prey that was assimilated by plants receiving both forms of nitrogen significantly increased the total concentration of nitrogen in pitchers.

There was no effect of the food web macroinvertebrates ($P = 0.944$) on the allocation of assimilated ^{15}N to belowground roots and rhizomes by *S. purpurea*. However, allocation patterns differed depending on the nitrogen source ($P = 0.026$). *S. purpurea* plants translocated more of the assimilated ^{15}N-prey below ground (9.45% ± 2.3%), relative to ^{15}N-NH_4NO_3 (6.6% ± 2.3%). This finding suggests that prey-N might be assimilated in a form other than completely mineralized NH_4 or NO_3 and might move throughout the plant in different ways from soluble nitrogen (as NH_4^+ and NO_3^-). For example, we have observed that *S. purpurea* can assimilate organic forms of nitrogen, such as glycine and other amino acids (J. Karagatzides, J. Butler, and A. Ellison, *unpublished data*).

Sarracenia purpurea retained >90% of its assimilated ^{15}N within aboveground pitchers and translocated <10% to belowground roots and rhizomes. In contrast, *S. alata* retained ~75% of assimilated ^{15}N within pitchers and *S. flava* only retained ~66% of assimilated ^{15}N within pitchers; the remainder was translocated below ground (species effect: $P < 0.0001$). This result was not unexpected, given the large rhizomes and relatively high (for a carnivorous plant) root : shoot ratio of *S. alata* and *S. flava*.

CONCLUSION

It was surprising that the presence of a complete brown food web within *S. purpurea* pitchers did not influence uptake of prey-N by the plant. Mosquito and midge larvae in this food web are involved in a processing-chain commensalism (Heard 1994), and other studies have shown that these nutrient-limited plants take up 40–60% of any available N (Bradshaw and Creelman 1984, Butler and Ellison 2007). Our results suggest that although the higher trophic levels actively process captured prey, the microbial component of the food web has a more important effect on nutrient availability for *S. purpurea*. Gotelli and Ellison (2006) also provide statistical evidence that strong microbial linkages control patterns of abundance in the *S. purpurea* food web. The importance of bacterial processing is supported further by the observation that its two congeners, which lack food webs, were able to take up the same amount of prey-derived N as *S. purpurea*. Although the higher trophic levels of the food web do not appear to directly assist in N acquisition by *S. purpurea*, they likely benefit the plant in other ways; for example adults of *F. fletcheri* are significant pollinators of *S. purpurea* (Ne'eman et al. 2006).

Although *S. purpurea* captures a variety of prey taxa, ranging from flies to small amphibians (Butler et al. 2005), ants represent the most common prey in northern populations (Newell and Nastase 1998). Ants, flies, and *D. melanogaster* have similar C:N ratios, but ants contain more chitin and may decompose somewhat more slowly than fruit flies. The food web might have had a greater role in uptake efficiency of nitrogen by the plant if ants had been used as a prey source, but we could not rear ^{15}N-enriched ants. However, whether or not a slower decomposition rate of ants in the absence of shredders would influence overall uptake of nitrogen across a growing season is not clear.

Further development of the *Sarracenia* microecosystem as a model with which to examine food web structure and function associated with various forms of "detritus" could greatly enhance our understanding of the links between detritus-based food webs, plant productivity, and producer-based food webs. Comparisons between the *Sarracenia* microecosystem and more typical detritus-based food webs in soil and aquatic systems also could yield new insights into the structure of microbial assemblages, the functional roles and redundancy of microbial species, and how bacteria link terrestrial to aquatic production in a wide range of ecosystems.

ACKNOWLEDGMENTS

This work was funded by collaborative grants to A. M. Ellison and N. J. Gotelli from the National Science Foundation (DEB 02-34710/02-35128 and DEB 05-41680/05-41936). We

thank Anthony D'Amato and Jonah Butler for assisting with these experiments, Derrick Mathias for kindly supplying *W. smithii* larvae, and David Post (Yale's Earth System Center for Stable Isotopic Studies) for analyzing our samples. Comments from Mike Kaspari, Stephen Heard, and two anonymous reviewers greatly improved this manuscript.

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