

LINKING THE BROWN AND GREEN: NUTRIENT

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

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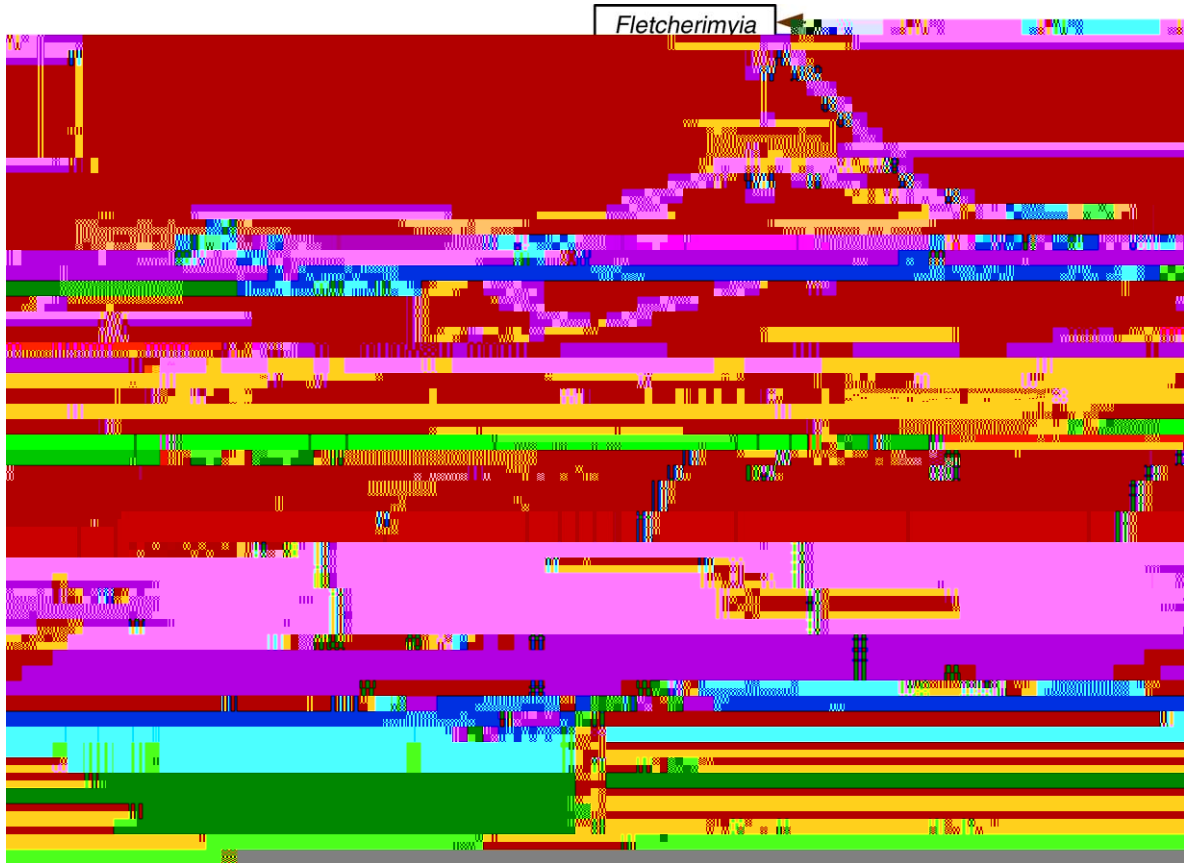


FIG. 1. A complex, multi-layered diagram representing a food web. The diagram is composed of numerous horizontal and vertical lines in various colors (red, yellow, green, blue, purple, cyan). At the top center, a box labeled 'Fletcherimyia' has an arrow pointing to a specific node in the network. The overall structure is dense and interconnected, suggesting a complex web of trophic relationships.

forms of nitrogen to the nutrient budget of *S. purpurea*, 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 *S. purpurea* 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 *S. purpurea* 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

S. 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,

To compare assimilation and subsequent translocation of prey-derived nitrogen by *S. purpurea* with other species, we applied the ^{15}N -prey treatment to four six-year-old seed-grown *S. purpurea* and four six-year-old seed-grown *S. purpurea* 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. purpurea* and *S. purpurea* 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* Brid.) in $10 \times 10 \times 10$ cm plastic pots. Pots were saturated at least twice each week with dd- H_2O .

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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 *S. purpurea* pitchers. To ensure that prey-derived nitrogen had in fact moved through the food web, we also dried and weighed all *F. caryocarpae* larvae at the end of the experiment, ground them individually, and analyzed them for ^{15}N abundance (*F. caryocarpae* 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 $100 \times (\text{g } ^{15}\text{N}_{\text{plant}}/\text{g } ^{15}\text{N}_{\text{fed}})$, where $\text{g } ^{15}\text{N}_{\text{plant}}$ and $\text{g } ^{15}\text{N}_{\text{fed}}$ 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 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*.

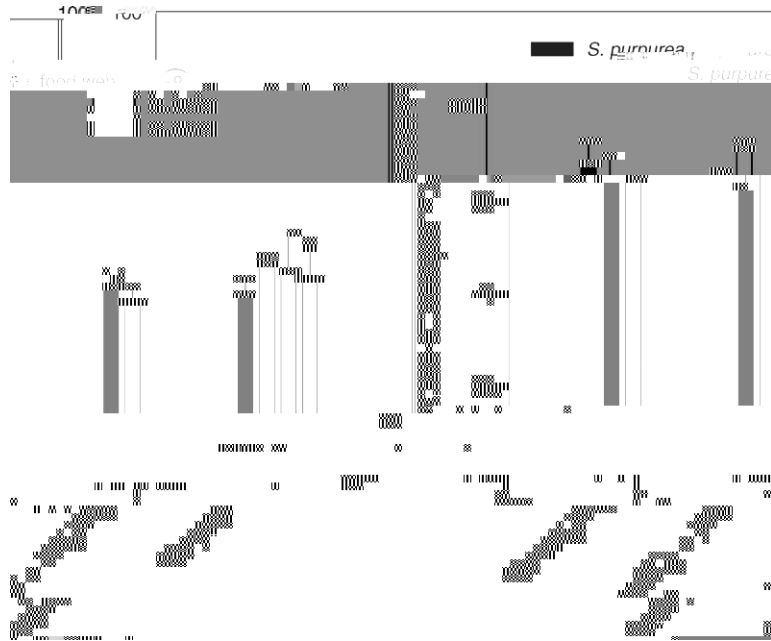


FIG. 2. Uptake efficiency of ^{15}N fed to *S. purpurea* as $^{15}\text{N-NH}_4\text{NO}_3$ and/or ^{15}N -prey with and without food webs in *S. purpurea*, and of ^{15}N -prey in *S. purpurea* and *S. exaltatum*. Bars are means, and error bars indicate one standard error of the mean from six replicate *S. purpurea* plants and four *S. exaltatum* and *S. purpurea* plants. Within *S. purpurea*, the presence of the food web had no significant effect on uptake efficiency ($F = 0.358$), but the form of nitrogen fed to the plants did ($F < 0.001$). There was no significant feeding treatment \times food web interaction ($F = 0.091$), nor did the three *S. purpurea* species differ in uptake efficiency when fed $^{15}\text{N-D}$ ($F = 0.959$).

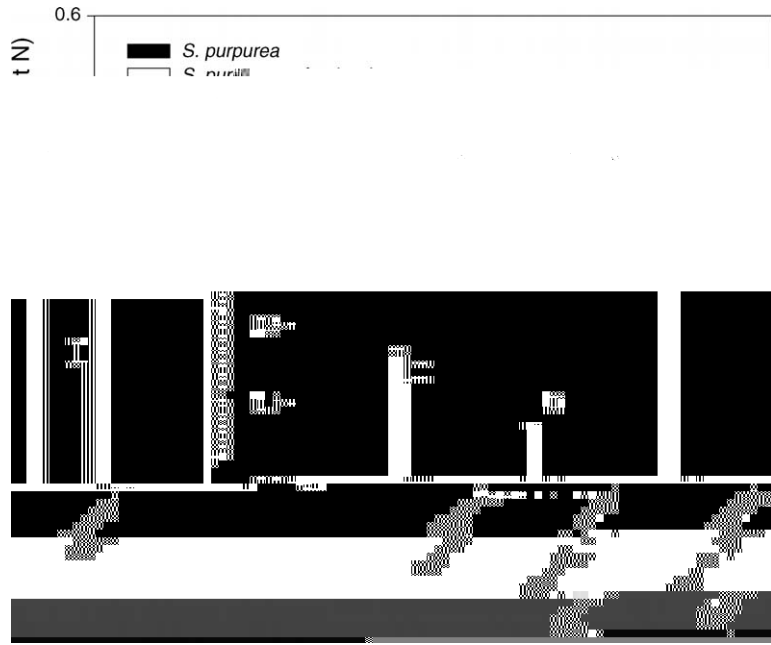


FIG. 3. Concentration of ^{15}N -tracer across all treatments for *S. purpurea* and *S. exaltatum* plants with and without food webs and for the ^{15}N -prey treatment for *S. purpurea* and *S. exaltatum*.

which . . . was fed excess prey. Thus, although plants receiving both prey and

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