



Population growth and production of *Habrotrocha rosa* Donner (Rotifera: Bdelloidea) and its contribution to the nutrient supply of its host, the northern pitcher plant, *Sarracenia purpurea* L. (Sarraceniaceae)

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Received 15 April 1998; in revised form 1 October 1998; accepted 9 October 1998

Key words: *Habrotrocha rosa*, nitrogen, phosphorus, population dynamics, predation, rotifers, *Sarracenia purpurea*

Abstract

The population growth and biomass production of the pitcher-plant (*Sarracenia purpurea* L.) inquiline, *Habrotrocha rosa* Donner (Rotifera: Bdelloidea), its consumption by other pitcher-plant inquilines, and its excretion of phosphorus (PO₄-P) and nitrogen (NO₃-N and NH₄-N), were investigated in laboratory experiments. Observed population growth and production rate of *H. rosa* were higher at pH 4 (2.3 rotifers d⁻¹) than at pH 3 (1.3 rotifers d⁻¹), 5 (1.9 rotifers d⁻¹), or 6 (0.8 rotifers d⁻¹). Populations of *H. rosa* are an abundant and reliable food source for larvae of the dipteran inquilines *Wyeomyia smithii* (Coq.) and *Blaesoxipha fletcheri* (Aldrich) that co-occur with *H. rosa* in *S. purpurea* pitchers. Abundance of *H. rosa* within a pitcher is negatively associated with abundance of dipteran larvae, and these larvae consume rotifers in direct proportion to rotifer density (Type I functional response). *Habrotrocha rosa* may also account for the majority of the plant's supply of N and P. An average population of rotifers in the field (~400 per pitcher) can excrete ~5.2 μg NO₃-N, ~3.91 μg NH₄-N, and ~18.4 μg PO₄-P per day into a single leaf, and excretion rate is independent of water pH. Over the six-month growing season of pitcher-plants in Massachusetts, U.S.A., we estimate that rotifers could supply 8.8–43 mg of N and 18.2–88 mg of P. These values far exceed the amount of N and P previously estimated to be supplied annually to the plants through insect capture or rainfall.

Introduction

The bdelloid rotifer *Habrotrocha rosa* Donner occurs as an inquiline in the fluid-filled pitcher-leaves of the carnivorous northern pitcher-plant, *Sarracenia purpurea* L. throughout the eastern United States and Canada (Bateman, 1987; Petersen et al., 1997). Although the aquatic inquiline communities of pitcher plants have been studied intensively for many years (e.g., Maguire, 1971; Addicott, 1974; Fish & Hall, 1978; Bradshaw, 1983; Fish, 1983), these studies have focused principally on the population dynamics and interactions among these communities' most common organisms, the dipteran larvae *Wyeomyia smithii* (Coq.) (Culicidae), *Metriocnemus knabi* Coq. (Chironomidae), and *Blaesoxipha fletcheri* (Aldrich)

(Sarcophagidae). Smaller inquilines, such as bacteria, protozoa, algae, and rotifers, are rarely discussed (but see Hegner, 1926; Addicott, 1974; Dudley, 1984 for notable exceptions), and even less frequently identified below class or ordinal level. Rotifers are common in inquiline communities of *S. purpurea* (Addicott, 1974; Petersen et al., 1997), and *H. rosa* may be largely restricted to this habitat (Petersen et al., 1997). The first goals of this study, therefore, were to document the population dynamics and biomass production of *H. rosa* and to assess its potential as a prey item for the larger dipteran larvae.

Comparatively little attention has been paid to the nutrient dynamics of either *S. purpurea* or its inquilines (Heard, 1994; Chapin & Pastor, 1995). Unlike other pitcher plants, *S. purpurea* does not di-

rectly digest prey captured in its pitchers (Juniper et al., 1989). Rather, the inquilines decompose the prey (Heard, 1994) and release into the pitcher fluid nutrients that are absorbed by the leaves (Hepburn et al., 1920; Plummer & Jackson, 1963; Plummer & Kethley, 1964). Rotifers, which feed principally on bacteria and particulate organic matter, are at the end of the "processing chain" (*sensu* Heard, 1994) that decomposes prey captured by *S. purpurea*. We hypothesized (Błędzki & Ellison, 1997) that *H. rosa* could contribute significantly to the nutrient budget of *S. purpurea* because rotifers excrete significant amounts of nitrogen (more than 70% as $\text{NH}_4\text{-N}$) and phosphorus ($\text{PO}_4\text{-P}$) via well-studied metabolic pathways (e.g., Ejsmont-Karabin et al., 1983; Ejsmont-Karabin, 1984; Wen & Peters, 1984; Gulati et al., 1995). The second goal of this study, therefore, was to measure N and P excretion rates by *H. rosa*. Because the pH of the fluid within *S. purpurea* pitchers is determined by that of local rainfall and also changes with pitcher age (Fish & Hall, 1978; Nastase et al., 1995), we further assessed nutrient excretion rates by *H. rosa* at pHs that spanned the range normally encountered under field conditions (pH 3-6). Together with the data on population dynamics of *H. rosa*, we estimated the minimum annual contribution of *H. rosa* to the nutrient supply of *S. purpurea*.

Materials and methods

Collecting sites

Rotifers were collected from *S. purpurea* growing at Hawley Bog, a 40 ha bog in a glacial depression in northwestern Massachusetts, USA (Moizuk & Livingston, 1966), and from *S. purpurea* growing at Granby Bog, a 10 ha bog 80 km SE of Hawley Bog.

Sample collection and abundance of *Habrotrocha rosa* in the field

Rotifers were collected during the spring and summer of 1996 and 1997. Fluid was removed from the pitchers using the suction apparatus described by Nastase et al. (1991). Liquid samples were placed in small plastic bags (whirl-paks) and transported immediately to our laboratory. Sample pH and volume were measured, and rotifers were counted using a Ward-Wildco counting wheel under a dissecting microscope at 225 \times . Number of dipteran larvae were counted under a dis-

secting microscope at 60 \times . We collected 31 samples in 1996 and 273 samples in 1997.

Population growth and production of *Habrotrocha rosa*

We studied population growth and biomass production of *H. rosa* at pH 3-6. This range spans that encountered in our field samples and those of previous investigators (Fish & Hall, 1978; Dudley, 1984). This wide range of pH results from variability in the pH of rain water that fills the pitchers, degradation of captured prey, and plant secretions (Fish & Hall, 1978). For each pH, we used 10 replicate 20 ml vials. Twenty-five rotifers were placed into each vial, and population size and production measured after 33 days. Rotifer cultures were fed once weekly with 0.06 ml of a ground fish food solution (0.25 g TetraMin flakes dissolved in 25 ml distilled water), or this same amount plus 0.02 ml of a baking yeast solution.

Daily production (biomass) of *H. rosa* was estimated from actual population counts multiplied by estimates of individual rotifer mass. To estimate mass of an individual *H. rosa*, we photographed populations of *H. rosa* at 60 \times using a Nikon F-3 camera attached to a Wild dissecting microscope. We randomly chose 50 rotifers from these photographs and measured their length, width and area using the SigmaScan image analysis package (SPSS Inc., Chicago, IL). Rotifer body area was then converted into volume (method of Ruttner-Kolisko, 1977) by integrating the area around the body width (computationally analogous to computing the volume of a cylinder from its maximal longitudinal-sectional area integrated around its diameter). Mean wet mass of *H. rosa* based on these volumetric measurements = 2.6 μg (assuming 1 μl = 1 μg , which is common for all rotifer species; Bottrell et al., 1976). The dry mass of rotifers usually is ~10% of its wet mass (Bottrell et al., 1976), but we observed that the soft-bodied *H. rosa* can contract rapidly and decrease its volume to <25% of its original size (osmobiosis, *sensu* Nogrady et al., 1993). Therefore, we estimated dry mass as 0.04 \times wet mass, as suggested by Ejsmont-Karabin (1974) for the similarly soft-bodied rotifer, *Asplanchna*. This yields a mean dry mass per *H. rosa* individual = 0.119 μg , which falls within the range of dry mass estimations for a wide variety of rotifer species (Yan et al., 1991).

Predation by Diptera larvae on *Habrotrocha rosa*

We measured predation rate of *Wyeomyia smithii* and *Blaesoxipha fletcheri* on *H. rosa*. *Wyeomyia* is a generalist filter feeder, while *B. fletcherii* is thought to feed principally on decaying corpses of insects that drown in the pitcher (Forsyth & Robertson, 1975). A single 3rd instar larva was placed in 25 ml of water (pH = 6) in a 50 ml centrifuge tube (approximately the same size and shape as a *Sarracenia* pitcher). Known quantities of rotifers (five replicates each of 10, 50, 100, 500 and ~1000) were added to the water; these concentrations spanned the densities encountered in the field (see Results, below). After 15 h, larvae were removed, and remaining rotifers were counted. In total, 25 replicates (five replicates each of five densities of rotifers) were run for each species of Diptera, along with 10 controls (no larvae).

Rates of N and P excretion by *Habrotrocha rosa*

Rotifers sampled from pitcher plants were cultured in 20 ml vials as described above. Rotifers were gently pipetted into a new vial to obtain ~5000 individuals. These were transferred onto small nets (15 μm mesh size), and washed with deionized water. The rotifers were then transferred into a watch glass filled with deionized water and maintained there for 10 min in order to remove food remnants from their intestines (cf. Ejsmont-Karabin, 1984). Prior to each experimental run, replicate 1 ml subsamples of 20 ml liquid were removed from the vials, and the rotifers in each subsample were counted with a counting wheel. For each experiment, ~5000 rotifers were transferred on 15 μm mesh nets into 300 ml watch glasses containing 100 ml of deionized water. Deionized water was used because the background concentration of N (especially $\text{NH}_4\text{-N}$) in the culture water was quite high. The concentration of nitrate ($\text{NO}_3\text{-N}$), ammonia ($\text{NH}_4\text{-N}$), and phosphate ($\text{PO}_4\text{-P}$) was measured in the water before rotifers were placed into the watch glasses and 5 h after the rotifers had been placed into the watch glasses. Nitrate concentration was measured using cadmium reduction spectrophotometry, ammonia with salicylate spectrophotometry, and phosphate with ascorbic acid spectrophotometry according to standard methods (APHA, 1985). This experiment was run at four pH levels (3, 4, 5, 6). Five replicates were used for each pH level, along with a parallel set of blank controls (no rotifers). All experiments were conducted at 22 °C, the median summer temperature in the field.

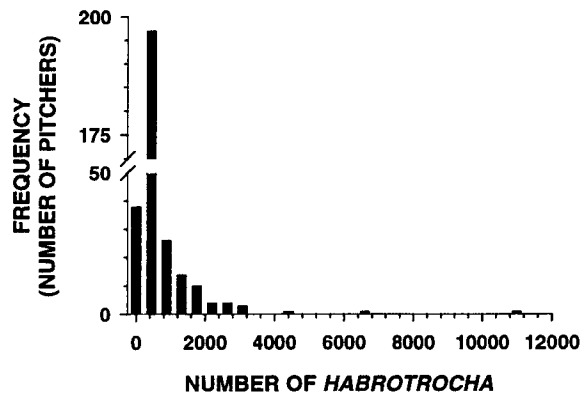


Figure 1. Frequency distribution of rotifer populations in individual pitcher leaves of *Sarracenia purpurea*. Samples taken in 1996 and 1997 are pooled in this figure.

Rotifers were re-counted at the end of reach experiment to check for dead or contracted individuals; these were rare.

Rotifers were not fed during these experiments. Nutrients excreted by starved rotifers are metabolized from food stored within their bodies as lipids (Nogrady et al., 1993). Nutrient excretion rates of starved rotifers are ~2 times lower than those for fed ones (Ejsmont-Karabin et al., 1983; Ejsmont-Karabin, 1984; Oude & Gulati, 1988; Ejsmont-Karabin & Wegleńska, 1989; Wen & Peters, 1994; Gulati et al., 1995). Thus, our estimates of nutrient excretion by *H. rosa* are minimal estimates of the amounts that could be excreted by them under field conditions in *S. purpurea* pitchers where food is relatively abundant.

Results

Abundance of *Habrotrocha rosa* in the field

On average, 388 ± 924 (SD) (range 0–10 960) *H. rosa* individuals were found in each pitcher (Figure 1). Mean volume of water in pitcher plants was 12.2 ± 10.3 ml (range 1–68 ml), giving an average density of 31.8 ± 51.7 rotifers ml^{-1} (31800 ± 51700 rotifers l^{-1}). Mean dry mass of *H. rosa* populations was 46.2 ± 109.9 μg per pitcher or 3800 $\mu\text{g l}^{-1}$.

Abundance of *H. rosa* in pitchers was not associated with water temperature, pH, or volume of standing water (Figure 2). Rotifer abundance was significantly and negatively associated with abundance of mosquito larvae (*Wyeomyia smithii*), but was independent of abundance of chironomid larvae (*Metriocnemus knabi*) (Figure 3). Normally, only one sar-

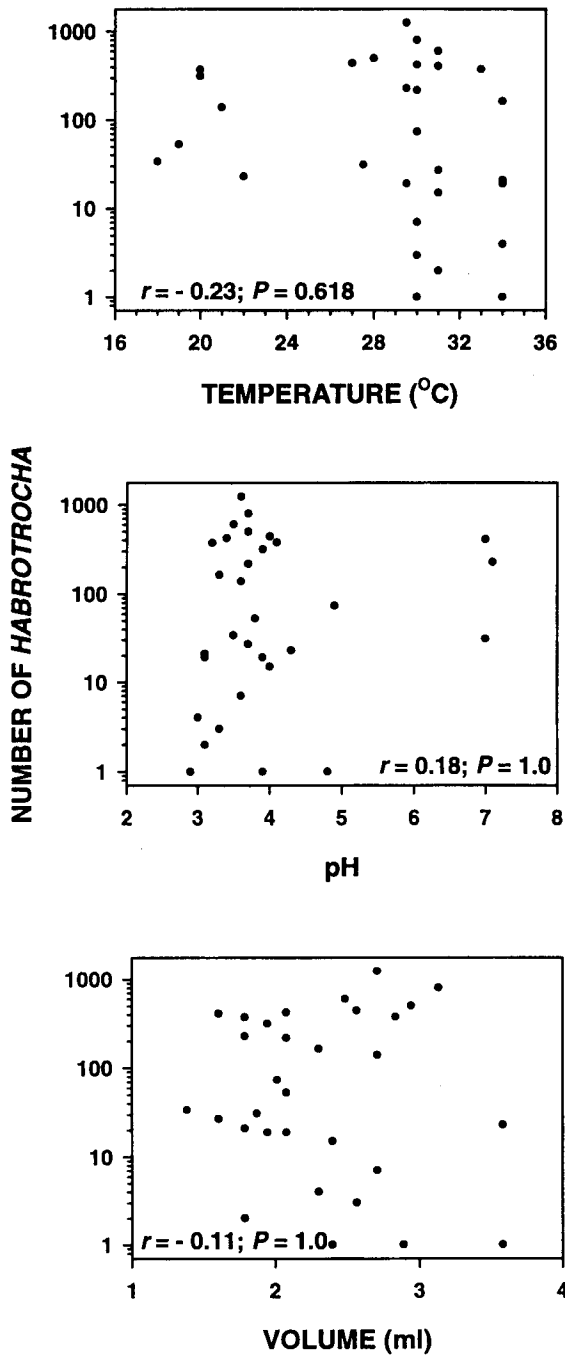


Figure 2. Relationships between pitcher fluid characteristics (water volume, temperature, and pH) and abundance of *Habrotrocha rosa*. Data shown are from 1996 only. Correlation coefficients and P-values for each relationship are shown on each panel.

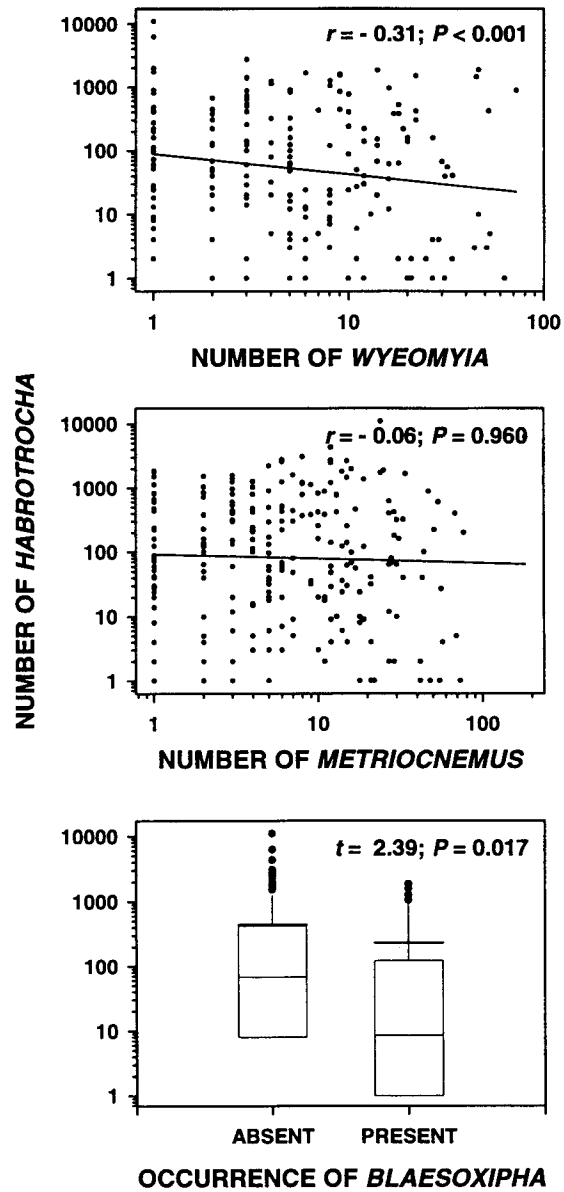


Figure 3. Relationships between abundance of *Habrotrocha rosa* and abundance of dipteran inquilines. Top two panels show relationships between abundances of *H. rosa* and mosquito larvae (*Wyeomyia smithii*), and between abundances of *H. rosa* and midge larvae (*Metriocnemus knabi*). Best-fit Type-II regressions are shown, and correlations and P-values are shown on each panel. Bottom panel illustrates box-plots of *H. rosa* abundance in the presence or absence of larva of the sarcophagid (*Blaesoxipha fletcheri*). In each box, median *H. rosa* abundance is indicated by the thin horizontal line, while mean *H. rosa* abundance is indicated by the thick horizontal line. Boxes extend to upper and lower quartiles of the *H. rosa* abundance distribution, whiskers to the upper and lower deciles, and all points beyond the upper decile are shown individually. Differences in *H. rosa* abundance with respect to presence or absence of *Blaesoxipha* were tested by t-test; t-value and P-value shown on panel. Data shown are for 1996 and 1997 pooled.

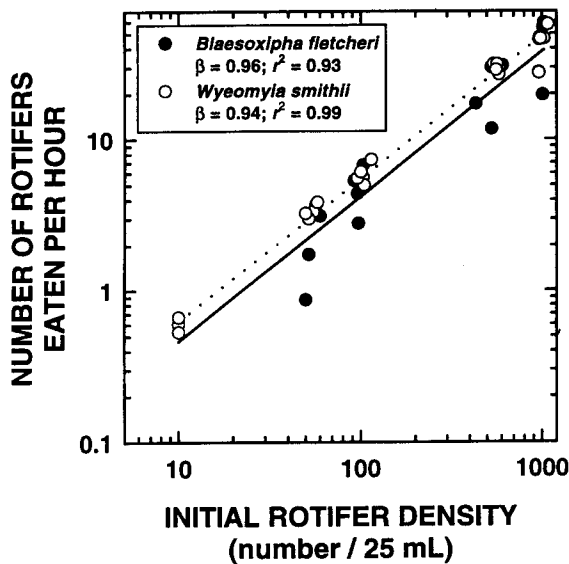


Figure 4. Predation rate by dipteran larvae on *Habrotrocha rosa*. Slope (β) and fraction of variance in consumption rate by each species explained by initial rotifer density (r^2) are given in the inset box.

cophagid larva (*Blaesoxipha fletcheri*) occurred in a pitcher, and when it was present, abundance of *H. rosa* was significantly reduced (Figure 3).

Population dynamics of *Habrotrocha rosa*

In laboratory cultures, population density (per 15 ml vial) after 33 days was significantly higher at pH 4 (1864 ± 560 ; $P < 0.01$, ANOVA) than at the other three pH levels, which did not differ significantly from each other (pH 3: 1073 ± 829 ; pH 5: 1548 ± 393 ; pH 6: 643 ± 208 ; Tukey's HSD post-hoc test for multiple comparisons among means). Assuming exponential growth of the populations, these values are equivalent to average daily specific growth rates of 1.3, 2.3, 1.9 and 0.8 rotifers d^{-1} , and average daily total biomass production rates of 3.9, 6.7, 5.6 and 2.3 $\mu g d^{-1}$ (both sets of values in pH 3 through 6, respectively).

Predation by Diptera larvae on *Habrotrocha rosa*

Both *Wyeomyia smithii* and *Blaesoxipha fletcheri* preyed on rotifers at a rate directly proportional to rotifer density (Type I functional response; Figure 4). Rotifer populations in control cultures (no predators) grew at the same rate as those in the population dynamics experiments, above (data not shown).

Table 1. Excretion rates ($ng\ rotifer^{-1}\ hr^{-1}$) of nitrate, ammonia and phosphate by *Habrotrocha rosa*, and background levels of these three nutrients in laboratory water. Values given are means \pm 1 SD, for all pH treatments pooled ($n = 20$). Results of *t*-tests are for comparisons between nutrient concentrations in rotifer cultures and controls

	NO ₃ -N	NH ₄ -N	PO ₄ -P
<i>H. rosa</i> present	0.9 \pm 0.59	2.3 \pm 1.46	2.8 \pm 2.07
Control	0.4 \pm 0.29	1.9 \pm 1.25	0.8 \pm 1.15
<i>P</i> (H_0 : rotifers = control)	0.001	0.34	0.001

Phosphorus and nitrogen excretion by *Habrotrocha rosa*

Habrotrocha rosa excreted measurable amounts of nitrate–nitrogen (NO₃-N), ammonia–nitrogen (NH₄-N), and phosphate–phosphorus (PO₄-P) (Table 1), and there were no effects of pH, water temperature, or dissolved oxygen concentration on excretion rates of nitrate, ammonia, or phosphate ($P > 0.10$, all cases, ANCOVA). Concentrations of nitrate and phosphate in rotifer cultures were significantly higher than background concentrations, while concentration of ammonia in rotifer cultures was not significantly higher than background (Table 1). Average net excretion rate per rotifer of nitrogen = 0.54 $ng\ hr^{-1}$ and of phosphorus = 2.04 $ng\ h^{-1}$. For an average population of 400 rotifers in 12 ml of water in a *Sarracenia* pitcher, this translates to 5.2 μg of nitrogen and 19.6 μg of phosphorus excreted per day. Observed excretion rates of nitrate, ammonia, and phosphate by *H. rosa* are within the range reported for other rotifer species (Table 2).

Discussion

Habrotrocha rosa is a common inquiline in fluid-filled pitcher leaves of *Sarracenia purpurea* (Bateman, 1987; Petersen et al., 1997), and our data illustrate that in the absence of dipteran larvae, *H. rosa* can reach very high densities. Both average rotifer density ($\sim 32000\ l^{-1}$) and maximal density ($\sim 900000\ l^{-1}$) are very high relative to density of rotifers normally encountered in lakes or reservoirs ($\sim 13000\ l^{-1}$; Błędzki, 1989; Błędzki et al., 1992).

Observed population dynamics and production rate of *H. rosa* are similar to those reported for other rotifer species (Le Cren & Lowe-McConnell, 1980). These rotifers are an abundant and reliable food source for

Table 2. Excretion rate of inorganic nutrients by various rotifer species. Mean body mass in μg dry mass, and mean excretion rates in $\mu\text{g hr}^{-1} \text{mg}^{-1}$ (dry mass)

Species	Mass	$\text{NO}_3\text{-N}$	$\text{NH}_4\text{-N}$	$\text{PO}_4\text{-P}$	Reference ¹
Habrotrocha rosa Donner	0.119	4.96	3.53	17.1	1
<i>Synchaeta kitina</i> Rousselet	0.011		129.00	40.9	2
<i>Keratella cochlearis</i> (Gosse)	0.013		43.1	35.8	2
<i>Conochilus unicornis</i> Rousselet	0.040		16.1	7.48	2
<i>Polyarthra vulgaris</i> Carlin	0.042		13.6	7.26	2
<i>Keratella quadrata</i> (Müller)	0.053		40.9	14.0	2
<i>Polyarthra dolichoptera</i> Idelson	0.069		1.77	0.626	2
<i>Synchaeta pectinata</i> Ehrenberg	0.280		1.62	0.707	2
<i>Asplanchna priodonta</i> Gosse	0.78		0.23	0.194	2
<i>Asplanchna priodonta</i> Gosse	1.67			0.06	2, 3
<i>Brachionus calyciflorus</i> Pallas	0.28		1.00	1.00	4
<i>Euchlanis dilatata lucksiana</i> Hauer	1.04		0.26	0.078	5
	0.65		0.77	0.18	5

¹References: 1 – this study; 2 – Ejsmont-Karabin, 1984; 3 – Hargrave & Geen, 1968; 4 – Ejsmont-Karabin et al., 1983; 5 – Gulati et al., 1989.

dipteran larvae that co-occur in *S. purpurea* pitchers (Figure 4). While these in vitro studies illustrate that the dipteran larvae could consume all available rotifers, field data (Figure 3) indicate that rotifers can persist in the presence of these predators. This persistence is likely due to habitat heterogeneity and micro-refugia within the pitcher and stratification of larvae with respect to water level (Fish & Hall, 1978). Predation by *Wyeomyia smithii* and *Blaesoxipha fletcheri* on rotifers has not been reported previously in studies of pitcher-plant inquiline community dynamics (e.g., Addicott, 1974; Farkas & Brust, 1985; Heard, 1994). The importance of rotifers relative to other food sources (bacteria, algae, protozoa, and carcasses of drowned insects) in the diet of these inquilines will be addressed in a future paper.

Because of their trophic position below the processing chain described by Heard (1994), excretion of nitrogen and phosphorus by *Habrotrocha rosa* may also account directly for most of the plant's supply of these essential nutrients. From data presented in Table 1 we estimate that an average population of rotifers can minimally excrete $5.2 \mu\text{g NO}_3\text{-N}$, $3.91 \mu\text{g NH}_4\text{-N}$ and $18.4 \mu\text{g PO}_4\text{-P}$ per day into a single leaf, rates comparable to those found for many other rotifer species (Table 2). Excretion of nitrate by rotifers has not been reported previously, as studies of N excretion by rotifers have focused principally on ammonia since the seminal paper of Jawed (1969). The ratio of N:P excreted by *H. rosa* is moderately lower, given its mass, than that reported for other rotifer species

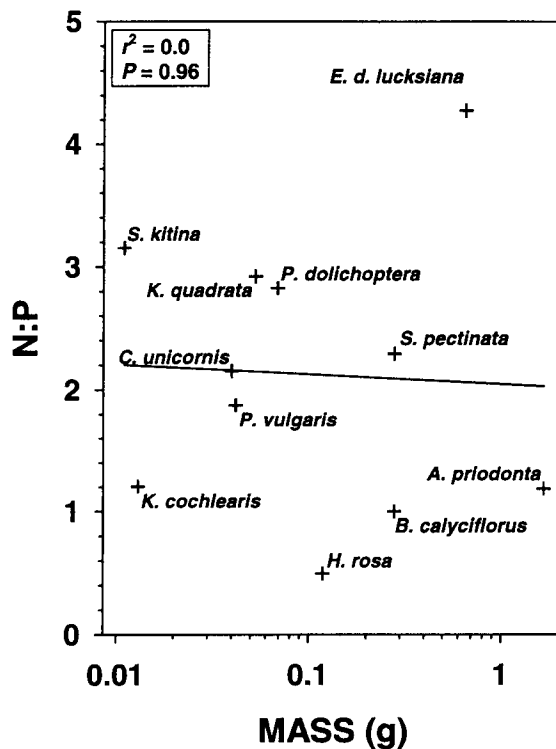


Figure 5. Ratios of N:P excreted by rotifers as a function of rotifer mass. Data derived from Table 1.

(Figure 5), although the expected relationship between rotifer mass and N:P ratio (Ejsmont-Karabin, 1984) was not found for the data shown in Table 1 ($P = 0.91$, all data; $P = 0.96$, *H. rosa* excluded). Further

investigation of the remaining >99% of rotifer species is required to determine if there is, in fact, a significant relationship between rotifer mass and nutrient excretion, as predicted by Ejsmont-Karabin (1984).

Over the six-month growing season in western Massachusetts, we estimate that rotifers can supply at a minimum, and in forms available for uptake by *S. purpurea*, as much as 3.3–16 mg P (as PO₄-P) and 1.6–7.9 mg N (0.9–4.6 mg NO₃-N and 0.7–3.3 mg NH₄-N) per leaf. Totals for whole plants, which produce 6 new pitcher leaves annually in Massachusetts (Fish & Hall, 1978) would range from 18.15–88 mg of P and 8.8–43 mg N. These values far exceed the amount of N and P previously estimated to accrue to the plants through insect capture (4.7 mg P and 3.75 mg N; Chapin & Pastor, 1995) or through rainfall (0.68 mg N; Chapin & Pastor, 1995). Because rotifers have been overlooked in previous studies of *Sarracenia* inquiline and nutrient dynamics, a recent review of mineral nutrition in carnivorous plants did not include the possibility that these animals could be the major supplier of N and P to *S. purpurea* (Adamec, 1997). Future studies of interactions between pitcher plants and their associated inquilines should expand their scope to include organisms other than dipteran larvae, and nutrient pathways beyond carnivory.

Acknowledgments

We thank the Massachusetts Nature Conservancy and Five Colleges, Inc. for permission to collect samples from Hawley Bog, and we thank Leon Chartier for permission to collect samples from the bog on his property in Granby. Elizabeth Smiley provided constructive comments on an early draft of this paper. This research was supported by NSF grant DEB-92-53743 and HHMI grant 71196-505002 to AME.

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