

PROJECT SUMMARY

A five-year research program is proposed to expand the theory of community assembly from its current base of correlative inferences to one grounded in process-based conclusions derived from controlled field and laboratory experiments. Northern pitcher plants, *Sarracenia purpurea*, and their community of inquiline arthropods and rotifers, will be used as the model system for the proposed experiments.

There are three goals to the proposed research.

- (1) Inquiline assemblages that colonize pitcher plants will be developed as a model system for understanding community assembly and persistence.
- (2) Field and laboratory experiments will be used to elucidate causes of inquiline community colonization, assembly, and persistence, and the consequences of inquiline community dynamics for plant leaf allocation patterns, growth, and reproduction, as well as within-plant nutrient cycling. Reciprocal interactions of plant dynamics on inquiline community structure will also be investigated experimentally.
- (3) Matrix models will be developed to describe reciprocal interactions between inquiline community assembly and persistence, and inquilines' living host habitats.

As an integrated whole, the proposed experiments and models will provide a complete picture of linkages between pitcher-plant inquiline communities and their host plants, at individual leaf and whole-plant scales. This focus on measures of plant performance will fill an apparent lacuna in prior studies of pitcher plant microecosystems, which, with few exceptions, have focused almost exclusively on inquiline population dynamics and interspecific interactions. Plant demography of *S. purpurea* will be described and modeled for the first time. Complementary, multi-year field and greenhouse experiments will reveal effects of soil and pitcher nutrient composition on leaf allocation, plant growth, and reproduction. Press and pulse field experiments will reveal effects of leaf age and size on inquiline community colonization and persistence. Markovian models of inquiline community assembly and pitcher plant leaf allocation that describe these reciprocal interactions will be fully integrated with a matrix model of pitcher plant growth. The results also will illustrate consequences of nutrient limitations in northern bogs by clarifying the relative importance of N- and P-limitation on growth of a common bog plant.

Most generally, the data gathered will enable the development, refinement, and testing of a mathematical model of community assembly in a dynamic habitat. This model will elucidate mechanistic links among community assembly, composition, and persistence; nutrient production and transfer; leaf ecophysiology; and plant growth. The results will lead to a more general and predictive understanding of community assembly and will be applicable to many other systems in which colonizing assemblages interact with living hosts, including other inquiline systems, host-parasite interactions, and plant-herbivore communities.

This proposal for Research at an Undergraduate Institution (RUI) will provide undergraduates with opportunities to participate in research and develop skills in mathematical modeling. The requested support will also facilitate improvements in the research and teaching infrastructure at Mount Holyoke College.

RESULTS FROM PRIOR NSF SUPPORT

A. M. Ellison

BSR-91-07195 — “RUI: Animal-plant interactions in mangrove communities” (12/91-5/95), \$162,000
DEB-92-53743 — Presidential Faculty Fellow (PFF) Award, “Marine Environmental Ecology: Teaching, Research and Conservation” (9/92-9/97 + no-cost extension to 9/98), \$500,000
DEB-97-41904 — “REU Supplement to DEB-92-53743” (6/97-8/97), \$5,000

Research accomplishments — These three awards supported a diverse set of projects addressing animal-plant interactions in tropical mangrove forests. Projects included: interactions between epibenthic marine invertebrates and mangrove growth and production (Ellison & Farnsworth 1992, Farnsworth & Ellison 1996a, Ellison *et al.* 1996); studies of insect herbivory in mangrove forests (Farnsworth & Ellison 1991, 1993, 1997); global biogeography of mangroves and associated gastropods (Ellison *et al.* 1998); growth and establishment of mangrove seedlings and saplings (Ellison & Farnsworth 1993, 1996a; Farnsworth & Ellison 1996b); responses of mangroves to global climate change (Farnsworth *et al.* 1997, Ellison & Farnsworth 1997); and evaluations of conservation and management of mangroves (Ellison & Farnsworth 1996b, Farnsworth & Ellison 1997) and other tropical wetlands (Ellison 1998). A full list of the 24 publications supported by these concurrent awards is given in section I of the Literature Cited section of this proposal.

Educational infrastructure and human resource development — The PFF award outfitted an undergraduate ecology teaching lab; supported construction in the greenhouse at Mount Holyoke of four mangrove mesocosms originally used for the research described by Ellison & Farnsworth (1997) and now used by introductory biology, intermediate ecology & evolution, and advanced ecology classes; and allowed for purchase of capital equipment used by the PI and undergraduates in ecology classes and by undergraduates who are engaged in independent research in the PI’s lab. In addition, support from the PFF award was used for curricular enhancement of the environmental studies program, which the PI has chaired since 1992. In accordance with requirements of the PFF award, the PI continued full teaching responsibilities (normally 6-9 contact hrs/wk) during the award period

These three awards supported 11 senior independent honors projects, 16 summer interns working in Belize and South Hadley, 10 work-study students (a total of 28 students) in the PI’s lab during 6 academic years and one sabbatical. These undergraduates are now in academic positions (1), graduate school (6), secondary school teaching (2), government jobs (2) or the private-sector work-force (15). Two students are still enrolled at Mount Holyoke. The PFF award supported a full-time technician in the PI’s lab. The PI’s primary collaborator, E. J. Farnsworth, completed her Ph.D. at Harvard University in 1997 with partial support from these grants. International collaborations were developed and are continuing with H. Díaz (IVIC, Caracas) and B. B. Mukherjee (Bose Institute, Calcutta).

N. J. Gotelli

BIR-96-12109 — “EcoSim: A proposal for null models software.” (8/96-7/97), \$50,000. This SGER grant supported initial development of computer software (EcoSim) for null model analysis in community ecology (**available free at <http://www.uvm.edu/~biology/Faculty/EcoSim/>**). The current version of EcoSim (1.10) is a Windows 95 application that features a graphical user interface, data base editor, data import and export, on-line help, and complete modules for analysis of niche overlap and species diversity.

DEB-91-18962 — “Ant lion zones: consequences of high-density predator aggregations.” (1/92-6/95), \$143,917. This study examined: effects of climate on aggregations of predaceous ant-lion larvae (Neuroptera: Myrmeleontidae) (Gotelli 1993); avoidance behavior of ant-lion prey (Gotelli 1996); and intra- and interspecific competition within ant-lion aggregations (Gotelli 1997). These studies resulted in 7 publications (see section II of Literature Cited), including two books (Gotelli 1995, Gotelli & Graves 1996). This award supported research projects by, and training of two graduate students, four undergraduate students, and eight high school students. The PI’s current research on ant lion movement strategies and population dynamics (DEB-96-15708) and work of the PI’s graduate student, Amy Arnett, on geographic variation in ant lion life history and population genetics (DEB-97-01122), both follow from results of projects supported by this award.

PROJECT DESCRIPTION

I. General Objectives

There are three goals to this proposed research. First, we develop inquiline assemblages that colonize pitcher plants as a model system for understanding community assembly and persistence. Second, we use a combination of field and laboratory experiments to elucidate causes of inquiline community colonization, assembly, and persistence, and the consequences of inquiline community dynamics for plant leaf allocation patterns, growth, and reproduction, as well as within-plant nutrient cycling. Third, we develop matrix models to describe reciprocal interactions between colonizing assemblages and their living host habitats. Taken together, our experiments and models will provide a complete picture of linkages between pitcher-plant inquiline communities and their host plants, at individual leaf and whole plant scales. By focusing on measures of plant performance, we will fill an apparent lacuna in prior studies of pitcher plant microecosystems, which have focused almost exclusively on inquilines (but see Bradshaw & Creelman 1984, Chapin & Pastor 1995). Our results also will illustrate consequences of nutrient limitations in northern bogs (Bridgman *et al.* 1996, Verhoeven *et al.* 1996, Bedford *et al.* 1998) by clarifying the relative importance of – and P-limitation on growth of a common bog plant. More generally, our data will allow us to further develop, refine, and test a mathematical model of community assembly in a dynamic habitat. This model will help expand the theory of community assembly from its current base of correlative inferences drawn from statistical analysis of observed patterns to one grounded in process-based conclusions derived from controlled experiments.

II. Theoretical Motivation

The search for general mechanisms of community assembly remains a major focus in community ecology (Drake 1990, Samuels & Drake 1997). Diamond (1975) first suggested that communities on islands could be characterized by a set of “assembly rules” – deterministic patterns of distribution and abundance controlled by interspecific competition. Other investigators have extended and refined these assembly rules, hypothesizing preferred assemblages of species (“favored states” of Fox & Brown 1993) and relatively constant proportions of species sets defined empirically or statistically (Wilson & Roxburgh 1994, Wilson *et al.* 1995). Supporters of assembly rules argue that competition, in the form of resource preemption or competitive hierarchies, structures communities (*e.g.*, Diamond 1975, Gilpin *et al.* 1986, Drake 1991). Critics of assembly rules assert that they are tautologies lacking predictive power (Connor & Simberloff 1979), or that evidence for consistent patterns of community structure, much less for assembly rules, is not

compelling (Wiens 1980). The research that we propose here presents a more powerful, explicitly experimental methodology for elucidating rules for community assembly.

Most research to date on community assembly has not been experimental, with the notable exceptions of laboratory microcosm studies by Drake (1991, Drake *et al.* 1993), Sommer (1991), Lawler (1993), and field studies of Weiher & Keddy (1995). A major controversy over null models and statistical analysis has dominated this literature for over 20 years (Connor & Simberloff 1979, Diamond & Gilpin 1982; Wilson 1995; Stone *et al.* 1996). One weakness of this literature is that interactions of species with habitats have been neglected (Gotelli & Graves 1996). Either habitat variation has been ignored (Connor & Simberloff 1979), or it has been treated as a simplistic constraint in null models (Gotelli *et al.* 1997). Community assembly does not take place in static habitats, however, and interactions between assembling communities and their habitat may generate deterministic assembly rules.

Biogenic structures can create considerable habitat complexity (Jones *et al.* 1997) that modifies subsequent colonization and generates community assembly rules (Dean 1981, Pringle 1985, Diamond 1986). Models of plant succession (*e.g.*, Connell & Slatyer 1977) recognize that environments change as a result of colonization. However, these models are phenomenological, and mechanisms of facilitation, inhibition, and tolerance do not elucidate interactions between *biotic* habitat structures and assembling communities. In this proposal, we develop Markov models of the reciprocal interactions between a colonizing animal community and a growing plant “host,” the northern pitcher plant, *Sarracenia purpurea*. We hypothesize that the animal community responds to changes in plant architecture, and plant architecture, growth, and reproduction in turn respond to nutrient production by the animal community.

III. Why Pitcher Plants?

Pitcher plants (families Sarraceniaceae, Nepenthaceae, Cephalotaceae) are excellent model systems for studies linking community assembly with habitat dynamics because these growing plants support species-specific inquiline communities in their pitchers (*e.g.*, Beaver 1983, Fish 1983). Leaves (Sarraceniaceae) or tendrils (Nepenthaceae, Cephalotaceae) are modified into pitcher-shaped organs (Arber 1941) that fill with rainwater and digestive enzymes. Nepenthaceae and southern (U.S.) species of Sarraceniaceae digest prey directly with plant-secreted proteolytic enzymes (Heslop-Harrison 1978), while *Sarracenia purpurea*, the focus of the proposed research, derives nutrients, primarily N and P, from prey that are decomposed by pitcher-inhabiting inquilines (Hepburn *et al.* 1920, Plummer & Kethley 1964, Williams 1966, Christensen 1976, Bradshaw 1983, Bradshaw & Creelman 1984, Heard 1994b, Chapin & Pastor 1995).

Numerous studies have described intra- and interspecific interactions among pitcher-plant inquilines (*e.g.*, Addicott 1974, Forsyth & Richardson 1975, Bradshaw 1983, Bradshaw & Holzapfel 1992, Mogi & Young 1992, Miller *et al.* 1994) and food web structures of these specialized communities (*e.g.*, Beaver 1983, Ratsirason & Silander 1996). Few studies, however, have addressed direct relationships between pitcher plants and their inquilines (Judd 1959, Plummer & Kethley 1964, Fish & Hall 1978, Bradshaw 1983, Bradshaw & Creelman 1984). Although Judd (1959) and Fish & Hall (1978) noted temporal variability in inquiline colonization of the northern pitcher plant *Sarracenia purpurea*, they attributed this observed variation only to leaf age. Cameron *et al.* (1977) noted that “studies on the fauna [are] hampered by the dual nature of the system where the life cycle of [the fauna] is superimposed on the seasonal cycle of the plant.” We propose to exploit this “dual nature of the system” to study experimentally inquiline community assembly, composition, and persistence in pitchers of *S. purpurea*, and to examine how changes in inquiline community structure affect leaf-scale ecophysiology, whole-plant development, and production of new “inquiline habitat” (pitchers). We will develop a stage-based matrix model of pitcher plant demography that synthesizes these processes.

Sarracenia produces two kinds of leaves: pitchers and phyllodes (Fig. 1; see also Macfarlane 1908, Mandossian 1966). Whereas pitchers collect water, host inquilines, capture prey, and accumulate nutrients, phyllodes are flat and are solely photosynthetic organs that probably are more efficient at photosynthesis than pitchers (Givnish *et al.* 1989) in part because pitcher morphology reduces surface area intercepting light (Kingsolver 1979). Despite detailed information on the anatomy of *Sarracenia* pitchers (Arber 1941, Adams & Smith 1977), no one has investigated conditions inducing phyllode production, or how they differ functionally from pitchers. Production of phyllodes not only limits opportunities for carnivory, but it also reduces habitat for inquiline communities. ***Our central question is: do inquiline communities supply nutrients to pitcher plants and change subsequent relative abundance of pitchers and phyllodes, and does this shift in turn change inquiline community assembly, composition, or persistence?***



Figure 1 — End-of-season (October 9, 1997) photograph of an individual *Sarracenia purpurea* at Hawley Bog, Massachusetts. All leaves produced by this individual in 1997 (8 red leaves in center) were phyllodes, while all leaves produced in 1996 (7 dead, grey leaves) were pitchers.

Givnish *et al.* (1984) developed a conceptual model (Fig. 2) to explain the restriction of carnivorous plants to sunny, nutrient-poor habitats. We adapt this model to generate hypotheses concerning the relative production of pitchers and phyllodes by a single *Sarracenia* individual.

In brief, Givnish *et al.* (1984) suggested that pitchers should be relatively inefficient at photosynthesis, but carnivory should be selected for as long as marginal photosynthetic costs of pitchers are outweighed by marginal gains in nutrient uptake deriving from carnivory. In high-sun environments such as open bogs, light levels are likely to be well above saturation, while extremely low nutrients available in bogs should

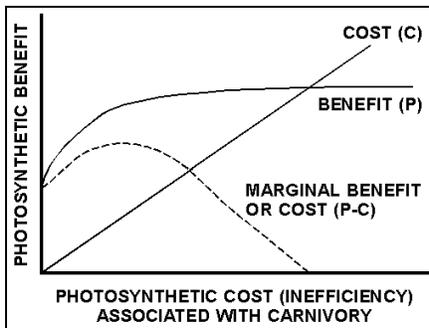


Figure 2 — Conceptual model (after Givnish *et al.* 1984) proposing that carnivory should evolve whenever the marginal difference between photosynthetic benefits of non-carnivorous leaves (P) and photosynthetic costs of carnivorous leaves (C) exceeds 0 (slope of dashed lines > 0). We adapt this conceptual framework as a physiological mechanism for within-plant phenotypic shifts from production of pitchers to phyllodes (or vice-versa) that underpins our plant allocation model.

lead to large marginal gains from carnivory. Surprisingly, key parameters needed to evaluate this model — simultaneous measurements of light levels, photosynthetic rates, nutrients available to roots, and those derived from carnivory — are unavailable in the literature for any carnivorous plant (see reviews by Lüttge 1983, Givnish *et al.* 1989, Adamec 1997). Moreover, since research on *Sarracenia* has been focused on inquiline community structure and dynamics, virtually all existing data are derived from single, individual pitchers (*e.g.*, Cameron *et al.* 1977, Weiss 1980, Joel & Gepstein 1985, Joel & Heide-Jørgensen 1985). However, nutrients are translocated among pitchers (Plummer & Kethley 1964) and initiation of leaf and inflorescence primordia are initiated one year before leaves and flowers fully develop. Thus, carbon gain and nutrient uptake in one year — which may be dependent on pitcher:phyllode ratio, carnivory, and inquiline activities — could affect the next year's pitcher:phyllode ratio, which in turn will affect possibilities for carbon gain, carnivory, and presence and abundance of inquilines. This observation also suggests the need for multi-year experiments; however, past experiments on effects of nutrient levels on pitcher plant growth have covered one growing season or less (Plummer & Kethley 1964, Bradshaw & Creelman 1984, Chapin & Pastor 1995).

We hypothesize that both pitcher architecture and inquiline community structure will exhibit strong reciprocal interactions because both parties change on similar within-season time scales. On an annual time-scale, the inquiline community may alter pitcher plant reproduction and population growth. We intend to quantify directly the effects of inquiline communities on plant demography and seed set. In the next section, we present results of pilot and on-going studies that demonstrate our capacity to work with these plants in the greenhouse and the field, and to obtain data necessary to calibrate our models. We then develop a transition-matrix model that links assembly, composition, and persistence of inquiline communities to production of pitchers, phyllodes, and plant fitness (reproductive output). We propose a set of field and laboratory experiments to parameterize the linkages of our model and elucidate ecological mechanisms driving these linkages.

IV. Preliminary Data

We collected preliminary data in 1997 from a population of >5000 *S. purpurea* plants growing at Hawley Bog, a 40 ha ombrotrophic bog in northwestern Massachusetts. Principal components analysis of bi-weekly pitcher censuses (May-September 1997) revealed three inquiline community types (Fig. 3): one dominated by mosquito (*Wyeomyia smithii*) and midge (*Metricnemus knabi*) larvae, one dominated by rotifers (*Habrotrocha rosa*) and mites (*Sarraceniopus gibsoni*), and one dominated by the larva of a sarcophagid fly (*Blaesoxipha fletcheri*). All three community types, along with empty pitchers, were present in varying numbers throughout the summer (Fig. 4).

These inquiline community types result from predation patterns by mosquito and sarcophagid larvae. Our laboratory feeding experiments showed that both species eat rotifers independent of the latter's density (Błedzki & Ellison 1997; see also Addicott 1974), thereby restricting rotifers to pitchers lacking larvae of these two dipterans. Sarcophagid larvae also eat mosquito larvae; thus mosquito larvae rarely are found in

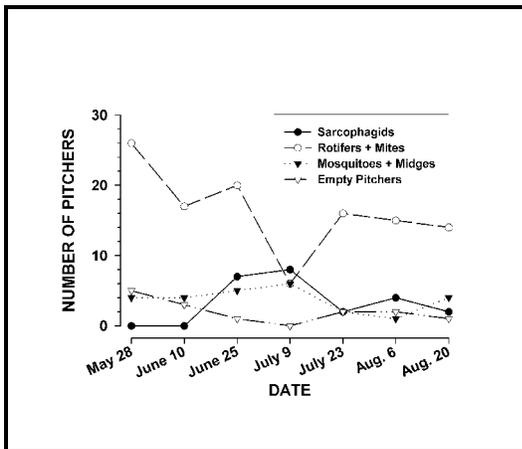


Figure 4 — Abundance of inquiline communities at Hawley Bog, summer 1997 ($n = 278$ samples).

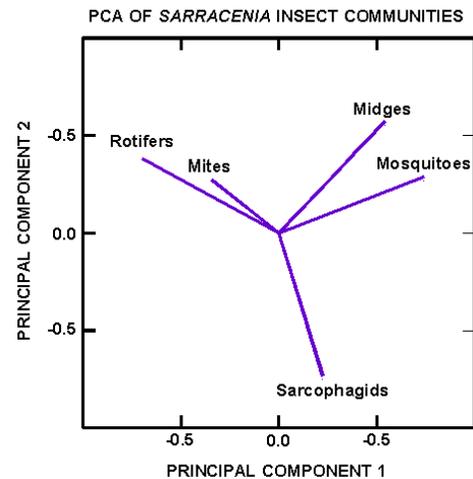


Figure 3 — PCA biplot of pitcher-plant inquiline communities at Hawley Bog ($n = 278$ samples; individual points not shown). Fifty-three percent of the variance in inquiline community structure is accounted for by the first two principal components.

pitchers inhabited by this large fly larva. The larger size of mites and midge larvae, and their tendency to inhabit pitchers bases prevented these two inquiline species from being eaten by either mosquito or sarcophagid larvae (see also Naem 1988, Heard 1994b).

Because rotifers are important sources of phosphate ($\text{PO}_4\text{-P}$) in aquatic ecosystems (e.g., Ejsmont-Karabin 1984, Wen & Peters 1994), we hypothesize that they provide P to *S. purpurea* pitchers. Our preliminary data suggest that *Habrotrocha* in pitcher plants excrete $2 \text{ ng } \text{PO}_4\text{-P } \text{L}^{-1} \text{ rotifer}^{-1} \text{ hr}^{-1}$; Błedzki & Ellison 1997). For an average population of 2,000 rotifers in 25 ml of pitcher liquor, this results in a net excretion of $2.4 \text{ } \mu\text{g } \text{PO}_4\text{-P/d}$, within the same order of magnitude as the concentration of $\text{PO}_4\text{-P}$ added to inquiline-free pitchers by Chapin & Pastor

(1995), the only other study of nutrient additions on *S. purpurea* growth. Thus, our data suggest that rotifers meet most or all of the demand for P by *S. purpurea*.

Rotifers and other inquilines decrease plant tissue N:P ratios of pitchers by 6% relative to phyllodes, but N:P ratios of both pitchers (8.8) and phyllodes (9.3) imply strong N-limitation (Verhoeven *et al.* 1996). Other data suggest that P availability normally limits plant growth in northeastern U.S. bogs (Bedford *et al.* 1998; see also Richardson 1985, Richardson & Marshall 1986), but we propose that inquilines produce enough P (*cf.* Plummer & Kethley 1964) to make N the limiting nutrient for *S. purpurea*. Nitrogen fixation by bacteria within pitchers ($150 \mu\text{g N pitcher}^{-1} \text{ day}^{-1}$; Prankeviccius & Cameron 1991), high atmospheric deposition (and pitcher retention) of $\text{NO}_3\text{-N}$ ($450 \mu\text{g/L}$ in rainfall at Hawley Bog), and release of N by other inquilines (*e.g.*, Bradshaw & Creelman 1984) appear to do little to ameliorate this N limitation. The high C:N ratios we observed in both pitchers ($\bar{x} = 33$, $n = 6$) and phyllodes ($\bar{x} = 38.1$, $n = 6$) similarly suggest that availability of N limits maximum photosynthetic rates (*e.g.* Field & Mooney 1986, Evans 1989, Ellsworth & Reich 1992). We measured very low maximum photosynthetic rates ($< 2.0 \mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of pitchers at Hawley Bog.

V. Matrix Models of Plants, Inquilines, and their Interactions

We propose to use a non-stationary, stage-based matrix model (Caswell 1986, Gotelli 1991) to predict pitcher plant population growth rate and size structure. Our model takes as inputs growth, survivorship, and reproduction of individual plants based on carbon and nutrient availability. Carbon fixation will be predicted by a second model describing an individual plant's allocation to phyllodes and pitchers. Nutrient availability has two components: soil nutrients and pitcher nutrients. Availability of pitcher nutrients depends not only on the number of pitchers, but also on inquiline community structure. The latter will be modeled as a Markov model of transitions among community states dependent on individual pitcher states. We hypothesize that these transitions are driven by reciprocal interactions plants and inquiline communities.

The population growth model (Fig. 5) has a time-step of one year and assumes that individual plants integrate within-year variance in (1) nutrient availability; (2) inquiline community composition; and (3) leaf physiology. The population growth model does not include explicit density dependence because pitcher plants probably are not limited by intraspecific competition over the range of densities typically observed in the field (Schwaegerle 1983). Pitcher plants will be classified as juveniles (J), non-reproductives (N), or reproductives (R). Juveniles are plants < 10 cm high and usually < 3 yrs old. Under optimal (greenhouse) conditions, *S. purpurea* can begin reproducing in its 3rd or 4th year, when new pitchers are normally ≥ 10 cm high, although reproduction in the field is rare before age 5. In the field, juveniles are easily distinguishable from potentially reproductive plants by non-overlap in their size distributions (Ellison, *unpublished*). Reproductive plants produce a single flowering stalk, and when pollinated, yield > 1000 seeds (Gotsch & Ellison 1997).

Only one of the transition probabilities in this model is constant. The probability that a reproductive plant reverts in the following year to the non-reproductive state (P_{RN}) equals $(1.0 - \text{annual$

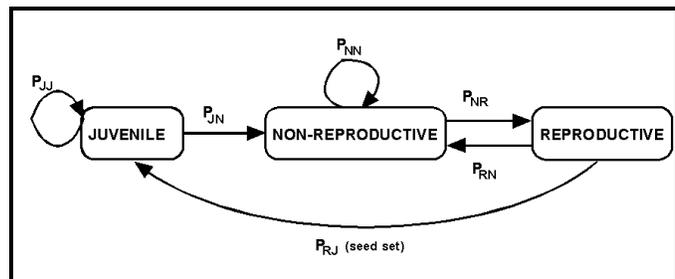


Figure 5 — Stage transition model for pitcher plants. Arrows indicate permissible transitions with an annual time step of 1 yr.

probability of mortality for reproductive plants) because plants produce no new leaves in years when they flower, and consequently rarely flower for two consecutive years. P_{RN} will be estimated from field monitoring of natural plant cohorts (Experiment 1, below). The other five transitions in the model are functions of soil and pitcher nutrient levels. These levels, in turn, depend on plant allocations to pitchers and phyllodes, and composition of inquiline communities within pitchers.

The leaf allocation model describes annual allocation among pitchers and phyllodes. Juveniles and non-reproductive plants must allocate their average annual production of 7 leaves (Ellison, *unpublished*) among pitchers and phyllodes. Phyllodes may be more efficient photosynthetically, but P_{max} is limited by N and only pitchers capture insects and nutrients for the plant. A non-reproductive plant can exist in one of 8 possible states (phyllodes:pitchers between 0:7 and 7:0). Hence, transitions between states can be modeled with an 8×8 transition matrix. Although all transitions are theoretically possible, we expect that most of the largest values in the matrix will fall near the diagonals, because pitcher plants usually add or remove only one phyllode or pitcher per year (Ellison, *unpublished*). This model will also have an annual time-step, and this transition determines the number of pitchers that will be available for inquiline colonization the following year. Initial estimates for transition probabilities will come from yearly censuses of a cohort of unmanipulated plants in the field (Experiment 1, below). We will also monitor leaf allocation in experiments that manipulate nutrients derived from soils and from inquiline processing chains (Experiments 2-4, below)

The inquiline assembly model classifies plant pitchers into four community states: empty; mosquitoes + midges; rotifers + mites; sarcophagids. We will use a series of Markov models (Usher 1979) to describe changes between these four states in a single pitcher. The time-step for the model will be two weeks, and the model will run for 10 time steps, which represents the typical growing season length for pitcher plants in western Massachusetts. We will use field census data (Experiment 5) to estimate transition probabilities between different inquiline community states. We will compare observed and predicted community states to test for the best fit of 3 different Markov models (Tanner *et al.* 1996). In a first-order model, transitions depend only on the current state of the assemblage. In a second-order model, transitions depend on both the current and the previous state of the assemblage. In a semi-Markov model, transitions depend on the absolute amount of time that an assemblage has been in a particular state. The semi-Markov model may be especially useful for this community because it will accurately describe transitions from Diptera-dominated assemblages in which larvae mature and leave pitchers after a given amount of time. Tanner *et al.* (1996) found that the equilibrium states for all three models were similar. However, the transient dynamics of the models were quite different, which will be important in our system because of the small number of time steps (10) within a season (see Fig. 4, above, for an example of non-equilibrium patterns of inquiline community abundance in a population of *S. purpurea*). These transient dynamics will be examined experimentally in Experiments 6-8.

VI. Hypotheses to be Tested

We propose to test two fundamental, reciprocal null hypotheses regarding linkages between community structure and temporally predictable habitat changes in pitcher-plant communities that derive from our models and observations to date:

- ***Inquelines produce no detectable changes in the ratio of pitchers to phyllodes and subsequent measures of plant performance: leaf nutrient status, photosynthetic rate, individual growth, seed production, or population growth.***

- *Seasonal variability in plant status — leaf size or age, ratio of pitchers to phyllodes, reproductive effort — has no impact on pitcher-plant inquiline community assembly, structure, or persistence.*

These two general hypotheses will be tested with a set of eight greenhouse and field experiments. Experiment 1 parameterizes the population growth model. The remaining seven experiments parameterize the other two models using ecological data collected on the interaction paths illustrated in Fig. 6. **A summary of all the experiments, the models and interaction paths they address, and the experimental time line is presented in Table 1 (page C-14).**

Path I — This path links inquiline communities with plant nutrient status, at the level of individual leaves, and will be addressed with Experiment 2. The results will be used to estimate parameters of our leaf allocation model.

Path II — This path links individual leaf nutrient status directly with whole-plant status, and will be addressed with Experiments 3-4. These experiments will provide additional supporting data for our leaf allocation model, and link whole-plant effects to our plant population growth model.

Path III — This path links individual pitcher status (size at opening and age) and whole-plant status (ratio of pitcher leaves to phyllode leaves) to inquiline community assembly, composition, and persistence. It will be examined with Experiments 5-6. The results will be used to estimate parameters of our inquiline assembly model.

Path IV — This path links individual pitcher status (size at opening and age) and whole-plant status with prey capture rates on which inquiline communities depend for sustenance. Experiments 7-8 will clarify the importance of inquiline processing chains in providing nutrients available for plant growth. The results define links among our models of inquiline assembly, leaf allocation, and plant growth.

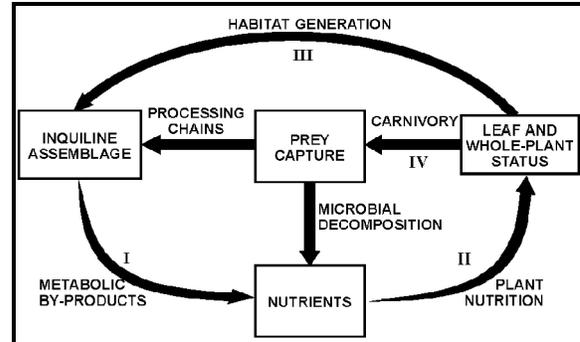


Figure 6 — *Explicit linkages between pitcher-plants and inquilines that will be examined by our proposed experiments. For clarity, we draw arrows representing unidirectional interaction paths, but we recognize, and our experiments test, that these interaction paths may be two-way. Processing chains, have been studied thoroughly by Heard (1994b). Direct microbial decomposition of prey independent of inquiline macrofauna, here incorporated into residual variance, will be the subject of a subsequent research proposal.*

VII. Experimental Design

Experiment 1: Field demographic monitoring. We will obtain baseline values for transition probabilities of the population growth model from two bogs, Hawley Bog in Massachusetts and Molly Bog in Vermont. Field data from two locations will allow us to assess the generality of our model beyond a single site. In April 1998, we will locate and permanently flag 100 randomly-selected juvenile plants (pitcher size < 10 cm) and 100 randomly-selected adult plants (pitcher size ≥ 10 cm) growing at each bog. These plants will be monitored annually for four years to determine annual stage transition probabilities (Fig. 5), flowering, and seed set. We also will establish ten, randomly-located 1-m² quadrats in each bog from which we will

remove all juveniles. Subsequent seedling recruitment in these quadrats will be used to estimate reproductive to juvenile (successful seeding) transition probabilities (as a function of local adult density).

Experiment 2: Inquilines, nutrients, and leaf allocation. This experiment tests the null hypotheses that inquilines have no effect on plant nutrient content, individual leaves, or whole plants, and that there are no interactions between nutrients derived from soil and pitchers. Three hundred and eighty-four plants will be grown hydroponically in sterile quartz sand in six 26×26 cm flats, each partitioned into sixteen 6×6 cm cells using plastic flat inserts. Seeds will be stratified for 6 weeks at 4° C prior to surface sowing (2 seeds/cell). Sown flats will be placed on greenhouse benches under natural light at 25° C and misted daily with distilled water until seedlings appear. We have obtained 85-100% germination of *S. purpurea* seeds within 3 weeks using this technique (Gotsch & Ellison 1997). Cells will be thinned to 1 plant/cell; extra seedlings will be transplanted into cells in which no germination occurs. Seeds will be planted in late February 1998, so that the proposed experiments can be initiated immediately upon receipt of grant support.

Once seedlings begin to produce pitchers in early summer, each flat will be randomly assigned to one of four soil nutrient treatments (*cf.* Christensen 1976, Cresswell 1991, Chapin & Pastor 1995, Adamec 1997): control (distilled water); N-only (150 mM NH₄Cl solution); P-only (20mM NaH₂PO₄); N+P (combination of above). Nutrients, along with balanced micronutrients (Chapin & Pastor 1995) will be mixed into distilled water and cells will be maintained at saturation by filling flats with the appropriate nutrient or control solution. Within a flat, each plant will be assigned at random (in a replicated latin-square design) to one of the three inquiline treatments identified in our field sampling (rotifers + mites; mosquito + midge larvae; sarcophagid larvae) or an empty control. Identical inquiline communities and densities or pitcher nutrients will be maintained in each plant during each of four successive growing seasons (a press experiment, *sensu* Bender *et al.* 1984).

Each pitcher on a plant will be filled half-way with distilled water, and then all pitchers on a given plant will be assigned to a single inquiline community treatment. Because pitchers vary in size and volume, inquiline communities will be assembled on a per ml (density) basis based on the average density of each species observed in our 1997 sampling: 1 mosquito per ml; 1 midge per ml; 80 rotifers per ml; 6 mites per ml; 1 sarcophagid per pitcher (independent of volume). Note that the density of mosquitoes and midges we observed in the field and that we will use in these experiments is well below that at which density-dependent interactions have been found to affect larval success or adult fecundity (Istock *et al.* 1976). First and second instar inquilines will be derived from current lab cultures, except for the sarcophagid, first-instars of which will be collected in mid-June. As larvae metamorphose into adults, they will be replaced to maintain constant densities of larvae throughout the growing season. As new pitchers are produced, they similarly will be half-filled with distilled water and identical inquiline communities will be introduced into the new pitchers. Inquiline communities will be fed 1g of housefly (*Musca domestica*) corpses once/wk. Greenhouse benches will be caged with fine screening (light reduction < 10%) to prevent unwanted colonization of pitchers or uncontrolled prey capture by pitchers. As plants outgrow their cells, they will be transplanted to prevent root-binding, and to avoid interference between leaves of adjacent plants.

This experiment will run for 4 years, which is the expected length of time required for *S. purpurea* grown from seed to reach reproductive maturity. We expect to see, and will document, ontogenetic changes in plant responses to inquiline community structure. Experimental manipulations will be carried out during normal growing seasons (April through October) each year, and plants and inquilines will be allowed to go dormant each winter (Paterson 1971, Paterson & Cameron 1982). Except for when seeds are germinated, the greenhouse will be unheated (to allow for winter dormancy), and natural light will provide normal photoperiods for these plants.

Response variables to be measured will be (1) pitcher-liquid nutrient concentration and pH (using ion-sensitive electrodes for $\text{NO}_3\text{-N}$, $\text{NH}_3\text{-N}$, and Ca, pH electrode, and standard spectrophotometric methods for $\text{PO}_4\text{-P}$ [APHA 1985, Fresenius et al. 1988]); (2) pitcher size (height, opening diameter, volume, dry mass); (3) tissue nutrient content (C, H, N, P, Ca, Mg, K) at the end of the summer (using a C-H-N analyzer, and atomic absorption spectrophotometry for P, Ca, Mg, K [Ma and Rittner 1979]); (4) rates of photosynthesis of phyllodes and pitchers (measured with a Li-Cor 6200 IRGA and custom-built cuvette; Fig. 7); (5) respiration rates of inquilines (measured with a Hansatech DW2/2 oxygen electrode); (6) rate of new leaf production and relative proportion of pitchers and phyllodes produced; (7) years to first reproduction and consequent seed set.

This experiment is set up as a split-plot design, and results will be analyzed using mixed-model ANOVA (for parameters measured only once, such as reproductive effort and success) or mixed-model repeated-measures ANOVA (for parameters measured annually for five years, such as growth or nutrient content). Total sample size ($n = 384$) will be sufficient to give statistical power > 0.90 , based on sample variances reported by Chapin and Pastor (1995). A power analysis of their published data suggests that they may have failed to find an effect of nutrient treatments because their statistical power was < 0.5 . All analyses will be done using S-Plus for Windows, version 4.0 (MathSoft 1997).

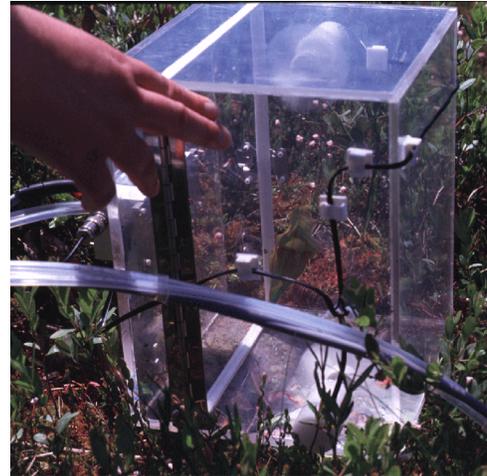


Figure 7 — Custom-built 8-L cuvette for measuring leaf-level and whole-plant photosynthesis of *Sarracenia purpurea*. A single pitcher is visible within it. The cuvette is constructed to Li-Cor specifications and connects to a Li-Cor 6200 photosynthesis system. A similarly constructed, 4-L cuvette also has been built for smaller plants.

Experiment 3: Leaf allocation and nutrients alone. This experiment tests the null hypothesis that nutrient content of the pitcher liquid by itself has no effect on plant growth, types of leaves produced, or leaf nutrient status and that there are no interactions between nutrients derived from soil and pitchers. This experiment will be structured in the same way as Experiment 2, but the inquiline community will be replaced with known concentrations of nutrient solutions: control, low N (15 mM), high N (150 mM), low P (2 mM), high P (20 mM), and the three possible N+P treatments that vary in N:P ratio (15:2, 15:20, 150:2). All pitchers will receive balanced micronutrients (Chapin & Pastor 1995). Like the previous experiment, there will be 6 flats/soil nutrient treatment, but in this experiment, there are 8 pitcher nutrient treatments (total number of plants = 384). All pitchers on a given plant will receive the same nutrient solution. Like Experiment 2, this experiment will run for 4 years as a press experiment (plants maintained in the same treatment each year). Measures of nutrient content and plant performance will be identical to those done in Experiment 2. ANOVA and repeated-measures ANOVA will be used to analyze the data.

Experiment 4: Leaf allocation and nutrients under field conditions. This experiment will replicate Experiment 3 in the field to examine whether pitcher-plants in the field respond to nutrients added directly to the pitchers in the same way as these plants respond in the greenhouse. One hundred and sixty plants growing in full sun on the bog mat at Hawley Bog will be selected at random in April 1998 for this experiment. Each plant will be assigned to one of the eight nutrient treatments described above for Experiment 3. All old leaves will be removed, and new leaves will be tagged as they are produced throughout the summer with small, numbered plastic rings (bird bands; National Band & Tag Co.) around their petioles. As leaves emerge, but before pitchers open, they will be covered with fine mesh (white

polyester chiffon) bags to exclude oviposition by inquiline adults, as well as prey capture by pitchers. Bags will also prevent attack of pitchers by herbivorous moth larvae (Brower & Brower 1971). These bags reduce light availability by 23%, but on sunny days ($> 2,000 \mu\text{mol m}^{-2} \text{s}^{-1}$), light reaching pitchers is still well above photosynthetic saturation for *S. purpurea* ($900 \mu\text{mol m}^{-2} \text{s}^{-1}$). As pitchers open, they will be filled half-way with the assigned nutrient solution (all pitchers on a given plant will receive the same nutrient solution). In this press experiment, treatments will be maintained at weekly intervals during 4 growing seasons, and plants will be measured (as described above). In addition, permanent, shallow wells (capped PVC tubing, 30 cm long, 1 cm inner diameter, perforated at 2.5 cm intervals) will be installed adjacent to each plant. Monthly during the growing season (April - October), pore water samples from these wells will be sampled and analyzed for pH, redox potential, $\text{NO}_3\text{-N}$, $\text{NH}_3\text{-N}$ and Ca. These soil nutrient data will further allow us to compare greenhouse and field soil nutrient conditions. Data from this experiment will be analyzed using ANCOVA (repeated measures where appropriate), with pitcher nutrient additions treated as main effects and local nutrient levels entered as covariates.

Collectively, the results from Experiments 1-4 will be used to estimate (1) transition probabilities for the population growth model; (2) effects of inquiline communities on pitcher liquor and leaf nutrient supply; (3) effects of these nutrients on individual leaf nutrient content and photosynthesis in greenhouse and field conditions; (4) the transition matrix of pitcher vs. phyllode leaf production as a function of soil nutrient supply and inquiline community activity; (5) the relative importance of soil- and pitcher-supplied nutrients on whole plant growth, primary productivity, and reproduction.

Experiments 5: Pitcher status and inquiline community persistence. This experiment tests the null hypothesis that inquiline community *persistence* does not vary with either mature pitcher size, which it reaches prior to opening, or its age (time since its opening). Although Judd (1959) and Fish & Hall (1978) found effects of pitcher age on inquiline colonization dynamics, they did not examine community persistence. Since inquiline communities likely interact with pitchers in different ways, we expect that their persistence in pitchers will feed back on nutrient cycling dynamics revealed by Experiments 2-4, as well as alter plant transition probabilities identified by Experiment 1. We will set up a 3-way balanced factorial pulse (*sensu* Bender *et al.* 1984) field experiment [Pitcher Size \times Age \times Inquiline Community]. There will be two levels of pitcher size (< 10 cm tall, ≥ 10 cm tall), three levels of pitcher age (newly-opened, 3 weeks old, 6 weeks old), and three inquiline communities (rotifer + mite; mosquito + midge; sarcophagid). Sample size is 10 plants per treatment combination (total $n = 180$ plants). Pitchers will be marked as they are produced, and bagged to exclude colonization. Bags will be removed at the appropriate time (when pitchers are just opened, 3 weeks after opening, 6 weeks after opening), half-filled with distilled water, and seeded with inquiline communities (on a per volume basis) as described in Experiment 2. Pitchers will then be re-bagged to prevent additional colonization during the course of the experiment. Inquiline communities will be fed 1g of housefly corpses weekly. Just before feeding, inquiline communities will be extracted (using the suction device described by Nastase *et al.* 1991), individuals counted, their larval instars noted, and the sample photographed on a grey background (for later determination by digitization of larval sizes); then the communities will be returned to the pitcher. One-ml subsamples will be collected and rotifer density determined in the lab. Response variables in this experiment will be inquiline survivorship, growth (mean time between instars), and percent eclosion. In addition, we will monitor pitcher liquid chemistry (pH, $\text{NO}_3\text{-N}$, $\text{NH}_3\text{-N}$, Ca, $\text{PO}_4\text{-P}$) as covariates that may contribute to observed variance in our inquiline response variables. Analysis will be by ANCOVA. This experiment will be replicated in two successive summers at Hawley Bog and Molly Bog (1999, 2000).

Experiment 6: Pitcher status and inquiline community assembly. This experiment tests the null hypothesis that inquiline community *assembly* does not vary with pitcher size or age. We will set up a 2-way balanced factorial field experiment [Pitcher Size \times Age] (factor levels as in Experiment 5; $n = 10$ plants/treatment combination). Again, pitchers will be marked as they are produced, and bagged to exclude colonization until the appropriate time (newly-opened, 3 weeks old, 6 weeks old), when bags will be removed. Natural colonization of inquiline communities will be monitored weekly, along with prey capture rates by pitchers and pitcher-liquor chemistry as described for Experiment 5. Numbers of phyllodes and pitchers on the whole plant will be noted throughout the experiment, as oviposition by sarcophagids, mosquitoes, and mites may be affected by pitcher:phyllode ratio (*cf.* Heard 1994a). Response variables of this ANCOVA design will be inquiline colonization rate, community composition, survival rates, and overall community persistence. In addition to leaf status, inquiline survivorship and community persistence are likely to be affected by prey availability, which will be monitored concomitantly. This experiment will also be replicated twice at Hawley Bog and at Molly Bog (in 1999 and 2000).

Concurrent with the experimental work on inquiline community assembly and persistence, we will monitor inquiline community *composition* of a separate, randomly-chosen group of 50 plants over the course of the same two growing seasons. We will sample these plants weekly as described above to determine background patterns in inquiline distribution and abundance. In particular, we are concerned that because of lack of exact concordance between insect phenology and plant leaf production rates, leaves used in Experiment 6 will not randomly “sample” the range of possible inquiline communities. Thus, this field monitoring will serve as a base-line control for this experiment.

The results of Experiments 5 and 6 will be used to assess the relationship between individual pitcher traits (size and age) and inquiline community assembly, composition, and persistence. These data will be used to calibrate the inquiline assembly model. Moreover, these results will provide additional field data on the effects of inquiline communities on pitcher-liquor chemistry. The field monitoring component of Experiment 6 provides a critical check for possible temporal bias of field manipulations.

Experiment 7: Prey capture, pitcher status, and pitcher:phyllode ratio. This experiment tests the null hypothesis that pitcher size and age, and pitcher:phyllode ratio has no effect on prey capture rate. Prey capture rates have been shown to decline with pitcher age (Judd 1959, Fish & Hall 1978, Wolfe 1981), but there have been no parallel experiments on capture rates or changes in prey composition with respect to pitcher size or whole plant status (pitchers:phyllodes). Our greenhouse populations provide us with the opportunity to examine relationships between prey capture rates by pitchers, pitcher size and age, and proportion of available pitchers per plant. Experiment 7 will be set up in the greenhouse as a two-way factorial design [Pitcher Size \times Age] stratified by phyllode:pitcher ratio (as available; minimum $n = 10$ /treatment combination) following the methods of Wolfe (1981). Individual plants will be enclosed in fine-screened cages, and 30 flies will be released into each cage. Capture rates (carcasses/pitcher/day) will be assessed after 24 hours by removing pitcher-liquor from each open pitcher and counting number of drowned flies. Each plant will be run on three successive days, once with lab-reared house-flies (*Musca domestica*), once with lab-reared fruit-flies (*Drosophila melanogaster*), and once with a mixed population of house-flies and fruit-flies (treatments in random order) to determine if capture rates differ with prey size and relative abundance. Prey density will not be varied, as both young and old leaves have a constant (but age-dependent) prey capture efficiency (proportion of prey captured) at prey densities < 200 flies (Wolfe 1981). Data will be analyzed using ANOVA. This experiment will be run once, in the summer of 2001.

Experiment 8: Prey capture rates in the field, pitcher status, and pitcher:phyllode ratio. This experiment tests the null hypothesis that pitcher size and age, and pitcher:phyllode ratio has no effect on prey capture rate in the field. We will select 60 random plants at Hawley Bog, stratified by leaf size and age (as in Experiment 6). For ten weeks, we will monitor prey capture rates by pitchers on a daily in order

to assure accurate identification of prey. We also will set up a network of pitfall traps and sticky-traps to determine composition and abundance of potential prey items, both of which may be sources of temporal bias in our results. Data will be analyzed using ANCOVA. Multivariate indices of potential prey composition will be developed and used as covariates in the analysis.

The results of Experiment 7 and 8 will be used to test for relationships between individual pitcher size and age, and relative pitcher availability on prey composition and capture rates. Since these prey form the basis of known processing-chain commensalisms among inquilines, and because the effects of inquiline processing chains on plant growth will have been assessed with Experiments 2-4, these last two experiments link our models of inquiline assembly, leaf allocation, and plant growth.

VIII. Feasibility

A 1,000 sq. ft. greenhouse at Mount Holyoke College will be dedicated to this research project. This greenhouse has temperature control and a reverse-osmosis system that delivers purified water needed to grow *S. purpurea*. Seeds for greenhouse experiments will be planted in February 1998, so that experiments can commence upon receipt of funding. Germination success is > 85% (Gotsch & Ellison 1997). Four seasons of experimental work will take plants from seedling through reproduction. Ellison's lab already maintains cultures of *Wyeomyia*, *Metriocnemus*, and *Habrotracha*, and is developing culture techniques for *Blaesoxipha* and *Sarraceniopus*. Field sampling techniques needed were used successfully in 1997 to monitor inquilines and prey captured by pitchers. Ellison is permitted to do field work at Hawley Bog, which is partially owned by Mount Holyoke College. Molly Bog is owned by the University of Vermont, and Gotelli will obtain permits to work there.

IX. Responsibilities of the PIs

Ellison will perform all greenhouse experiments, and field work at Hawley Bog. Gotelli will conduct field work at Molly Bog. Gotelli will develop and test the matrix models of plant growth, leaf allocation, and inquiline assembly, and oversee plant nutrient analysis at the University of Vermont. Ellison will train and mentor undergraduates who are involved with field and laboratory work. In years 3, 4, and 5 of the grant, these students will travel each year for two weeks to the University of Vermont, where Gotelli will teach a short course in ecological modeling using the data generated from this project (see RUI Impact Statement, page C-15). Mt. Holyoke and the University of Vermont are within a 4 hour car drive of one another, and each year the PIs will make several visits back and forth for data collection and analysis. Both PIs will share equally in the analysis and publication of results.

X. Significance of the Proposed Research

Our proposed research focuses on reciprocal interactions between a colonizing inquiline community and its growing host habitat, the pitcher plant *Sarracenia purpurea*. Plant demography of *S. purpurea* will be described and modeled for the first time. Our complementary, innovative, and multi-year field and greenhouse experiments will reveal effects of soil and pitcher nutrient composition on leaf allocation, plant growth, and reproduction. Press and pulse field experiments will reveal effects of leaf age and size on inquiline community colonization and persistence. Markovian models of inquiline community assembly and pitcher plant leaf allocation that describe these interactions will be fully integrated with our model of pitcher plant growth. Most generally, our proposed research will elucidate mechanistic links among community assembly, composition, and persistence; nutrient production and transfer; leaf ecophysiology; and plant growth. The results will enhance our general understanding of community assembly and will be

applicable to many other systems, including other inquiline systems (*e.g.*, Maguire 1971, Koukouras 1992), host-parasite interactions, and plant-herbivore communities (*e.g.*, Waltz & Whitham 1997), in which colonizing assemblages interact with living host.

Table 1 — Summary of proposed experiments, including growing seasons in which each experiment will be conducted. All greenhouse experiments will be replicated in the field at Hawley Bog, while stand-alone field experiments will be conducted at both Hawley and Molly Bogs.

Exp.	Location and Date	Path	Model	Protocol	Response variables
1	Hawley & Molly Bogs 5/98-10/01		Plant population growth	Demographic monitoring.	Transition probabilities between juveniles, non-reproductive adults, and reproductive adults; seed set.
2	Greenhouse 5/98-10/01	I	Leaf allocation	Soil nutrients (4) × Inquiline communities (4) in a repeated-measures, split-plot design.	Leaf-level: pitcher-liquid nutrient concentration NO ₃ -N, NH ₃ -N, PO ₄ -P, and Ca) and pH; leaf tissue nutrient content; P _{max} of leaves and respiration of inquilines. Whole-plant level: rate of new leaf production; relative proportion of pitchers and phyllodes produced; years to first reproduction and consequent seed set.
3	Greenhouse 5/98-10/01	II	Leaf allocation	Soil nutrients (4) × Pitcher nutrients (8) in a repeated-measures, split-plot design.	
4	Hawley Bog 5/98-10/01	II	Leaf allocation	Pitcher nutrients (8) × Soil nutrients (natural, measured) × Plant stage (2) in a repeated-measures ANCOVA design.	
5	Hawley & Molly Bogs 1999, 2000	III	Inquiline assembly	Leaf size (2) × Leaf age (3) × Inquiline communities (3) in a balanced, factorial design.	Inquiline community persistence, measured as survivorship, growth, and % eclosion. Pitcher liquor chemistry (pH, NO ₃ -N, NH ₃ -N, PO ₄ -P, Ca).
6	Hawley & Molly Bogs 1999, 2000	III	Inquiline assembly	Leaf size (2) × Leaf age (3) in a balanced, factorial design.	Inquiline community assembly, measured as colonization rate of the different species, and persistence (as in Experiment 5). Temporal bias in this experiment will be assessed with a parallel set of observations of unmanipulated plants.
7	Greenhouse 2001	IV	Leaf allocation & Inquiline assembly	Leaf size (2) × Leaf age (3) in a balanced, factorial design, stratified by phyllode:pitcher leaf ratio.	Prey capture rate (carcasses/pitcher/day) of monospecific and mixed populations of house-flies and fruit-flies.
8	Hawley Bog 2001	IV	Leaf allocation & Inquiline assembly	Leaf size (2) × Leaf age (3) in a balanced, factorial design, stratified by phyllode:pitcher leaf ratio.	Prey capture rates. Temporal bias in this experiment will be assessed with a network of pitfall traps and sticky traps to monitor composition and abundance of possible prey species.

**IMPACT OF THE PROPOSED RESEARCH ON THE EDUCATIONAL INFRASTRUCTURE AT
MOUNT HOLYOKE COLLEGE**
(RUI Impact Statement)

The proposed research will have three substantive, positive impacts on undergraduate biology education at Mount Holyoke College. First, this research project will provide opportunities for undergraduate summer research, year-long independent projects leading to senior honors theses, and term-time work-study employment. Four of the proposed experiments (Experiments 5-8) could be done as summer student research projects leading into year-long senior independent projects. Experiments 6 and 8 are well-designed for undergraduate collaborations: one student responsible for the experimental work and the other responsible for independent observation/monitoring protocols designed to account for possible experimental bias. Experiments 1-4 require long-term attention and oversight by a single individual (hence the budget request for continued support for the technician in Ellison's lab at Mount Holyoke), but similarly provide opportunities for summer research collaborations. The long-term nature of Experiments 1-4 will let students build on each other's work, encouraging a sense of continuity among student researchers. In addition, we encourage undergraduates to initiate projects related to but independent of the proposed core research (funding for such projects is available directly to undergraduates through other grants and endowed funds at Mount Holyoke). We note in particular that one undergraduate, Sybil Gotsch, obtained independent funding (in 1996) for her study of germination of *S. purpurea* seeds that has been submitted for publication, and which led to the development of the germination protocols used for Experiments 2, 3, and 7. Finally, work-study students will be employed to maintain lab cultures of inquilines and prey. All students working on this project will be incorporated into general activities of term-time and summer research programs in Biology, Chemistry, and Mathematics at Mount Holyoke. These include training in "science survival skills" (e.g., Feibelman, 1993) through participation in a 3-day summer workshop (supported by a grant from Howard Hughes Medical Institute), end-of-summer poster and oral presentations, participation in the annual undergraduate science symposium at Mount Holyoke, and attendance at regional and national meetings.

Second, this research project will provide opportunities for student participants to develop skills in ecological modeling. During the last three years of the grant, all students involved in these projects annually will spend two weeks during Mount Holyoke's January intersession at the University of Vermont in an intensive short-course taught by the co-PI (Gotelli). The short course will teach students to use EcoSim and MatLab to model community processes. Using the community assembly model developed herein as a base, students will explore mathematical models commonly used in studies of community ecology (Gotelli 1995, Gotelli & Graves 1996). Since there is no modeling course at Mount Holyoke, this short-course will provide a new curricular opportunity for ecology students enrolled at Mount Holyoke. Working at the University of Vermont also will provide Mount Holyoke students with possibilities of working with graduate students and post-docs, role models in short supply at Mount Holyoke.

Finally, the greenhouse populations of pitcher plants and the associated infrastructural modifications to the ecology research wing of the Mount Holyoke conservatory will continue to be used by students and faculty well beyond the term of this grant. Prior grants to the PI were used to develop mangrove mesocosms that are now used in introductory biology, a sophomore course in ecology & evolution, and a senior seminar in ecology. Similarly, pitcher plants are ideal model micro-ecosystems that can be used for teaching concepts in areas ranging from plant physiology through community structure. Investments in the basic research projects proposed here will pay off not only in publications by the PIs and their students, but also in longer-term improvements to the undergraduate biology curriculum at Mount Holyoke College. Both Mt. Holyoke and the University of Vermont are dedicated to high-quality undergraduate teaching. Ellison's PFF award was for excellence in teaching, research, and service. Gotelli was recently awarded the Dean's Lecturer for excellence in undergraduate teaching and research.

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