NITROGEN DEPOSITION AND EXTINCTION RISK IN THE NORTHERN PITCHER PLANT, *SARRACENIA PURPUREA*

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Abstract. Chronic nitrogen deposition may affect the long-term survival of plant populations. The northern pitcher plant, *Sarracenia purpurea*, is a model system for forecasting extinction risk in the face of increasing nitrogen deposition. Uptake of N occurs directly from pitcher leaves, which fill with rainwater and prey, and accumulate nutrients. We monitored the demography of two populations of *S. purpurea* in ombrotrophic bogs of northern New England (USA) and described population growth with a four-stage matrix model. Growth, survivorship, and reproduction were in close balance, and the model predicted population growth rates close to zero, with long doubling times. In a life-table response experiment, we manipulated in situ concentrations of nitrogen and phosphorus in pitcher plant leaves. At high levels of N and high N:P ratios, population growth rates were significantly depressed. Using local N-deposition records, we forecast different N-deposition scenarios and built a nonstationary population growth model, in which a different transition matrix at each time step reflected the current deposition regime. Autocorrelation in the time series of N deposition rates generated periodic increases in population size superimposed on long-term trends of exponential decline. For a 1% annual increase in N deposition rates, this model predicted a substantial risk of extinction at 100 yr (0.38–0.70), with an estimated population survival time of 160–180 yr. Although slow-growing populations of *Sarracenia* can buffer substantial environmental change, chronic increases in N deposition rate threaten population persistence.

Key words: demographic study; extinction risk; life-table response experiment; long-lived perennial; matrix model and population growth; N:P ratio; nitrogen deposition; ombrotrophic bogs; pitcher plant, northern; population growth; Sarracenia *population vs. increased N deposition.*

INTRODUCTION

Small increases in nitrogen (N) deposition often enhance plant growth and productivity (Tilman 1987), but chronic increases have many detrimental effects, including nutritional deficiencies (Van Dijk and Roeloffs 1988), decreased growth (Spink and Parsons 1995), and decreased cold tolerance (DeHayes et al. 1999). At the ecosystem level, increased N deposition results in N saturation and decreased N retention (Aber et al. 1998, *in press*). Less attention has been paid to the effects of N on plant population dynamics, even though population biology links effects at the individual plant level with ecosystem responses. For example, altered demographic rates can increase extinction risks (Menges 1992, Schemske et al. 1994) and change biodiversity (Heil and Diemont 1983, Woodin and Farmer 1993), with consequences for ecosystem dynamics (Naeem et al. 1994, Schwartz et al. 2000).

The northern pitcher plant, *Sarracenia purpurea*, is a model system for understanding consequences of N deposition on population dynamics. *S. purpurea* offers

three advantages for this kind of study. First, *S. purpurea* is a long-lived (>50 yr) perennial plant; its current population structure is a demographic snapshot of conditions that were present several decades ago, opening a window onto how environments for population growth have changed (Doak and Morris 1999). Second, pitcher plants typically grow in N-poor ombrotrophic bogs (Givnish et al. 1984) that receive the majority of their nutrients from precipitation (Hemond 1983, Damman 1990). Finally, the carnivorous *S. purpurea* collects rainwater and prey in its pitchers (Juniper et al. 1989), but prey account for <10% of the plant's N budget (Chapin and Pastor 1995, Bledzki and Ellison 1998, Ellison and Gotelli 2001). Hence, if N is an important determinant of population processes, the demography of *S. purpurea* should be a function almost entirely of local N deposition.

Despite these advantages, modeling population dynamics and forecasting extinction risk of a long-lived perennial plant is challenging. We synthesized results of demographic censuses and a nutrient-addition experiment to model population growth and extinction risk. We combined the experimental results with annual N-deposition data to create a nonstationary matrix model in which environmental conditions change each time step. This life-stage simulation analysis (LSA; Wisdom et al. 2000) allowed us to forecast extinction

risks and persistence times of *S. purpurea* populations as annual N deposition rates gradually change.

MATERIALS AND METHODS

Demographic survey

Sarracenia purpurea is a rosette-forming perennial plant that ranges throughout Canada and the eastern United States, where it grows in bogs, nutrient-poor fens, and seepage swamps. Among the 8–9 species of *Sarracenia*, *S. purpurea* is the only one that collects water in its tubular leaves (Folkerts 1999). In northern New England, leaves are produced approximately every 20 d (Fish and Hall 1978) and persist for one or two years. Pitcher plant leaves attract arthropod prey that are decomposed by a diverse inquiline community (Addicott 1974, Heard 1994). As in other carnivorous plants, *S. purpurea* has a weakly developed root system (Juniper et al. 1989), and there is little evidence of fragmentation or asexual reproduction. At our study sites, we have observed that *S. purpurea* does not reproduce until rosette diameters reach 10 cm. Plants produce a single-flowered inflorescence that is pollinated by large bees and flies (Burr 1979). Capsules mature in the fall and yield on average 1000 seeds. Seeds germinate readily (Ellison 2001), but there is no evidence of a persistent seed bank. Rosettes are long-lived and may persist for 30–50 yr.

We studied *S. purpurea* populations at two ombrotrophic ("rain fed") level bogs: Molly Bog (Vermont, USA; 44° N, 72° W) and Hawley Bog (Massachusetts, USA; 42° N, 72° W). Like most ombrotrophic bogs in northeastern North America, Hawley and Molly Bogs formed in local depressions that resulted from glacial action (Moizuk and Livingston 1966). Although both bogs are ombrotrophic, Molly Bog is classified as a pond-margin bog, whereas Hawley Bog is classified as a stream-headwaters bog (Kearsley 1999).

At each site, we tagged 100 juvenile (rosette diameter <10 cm) and 100 adult (rosette diameter ≥10 cm) plants in April 1998. Plants were haphazardly selected by meandering across the center 300 m² of the bog mat at each site and tagging all plants that were clearly identifiable as discrete rosettes. The sample populations at the two sites did not differ in initial morphology or reproductive rate (A. M. Ellison and N. J. Gotelli, *unpublished data*). We censused each plant, measured its rosette diameter, and recorded its flowering and fruiting status annually in 1998, 1999, and 2000. These data allowed us to estimate annual transition probabilities of growth, stasis, reproduction, and mortality that form the inputs for our stage transition matrix model.

Nutrient-addition experiment

To examine the effects of nutrients on demography, we experimentally manipulated N and P concentrations in the pitcher water of juvenile and adult plants at Hawley Bog. In this life-table response experiment (LTRE; Caswell 1989), we measured growth, mortality, and reproduction, and estimated population growth rates of plants in each nutrient treatment. We haphazardly selected an additional 90 adult and 90 juvenile plants and randomly assigned them to one of nine different nutrient treatments: two control treatments (distilled H_2O or 10% concentration of micronutrients from Hoagland's solution); two N treatments (0.1 mg NH_4-N/L or 1.0 mg NH_4-N /L as NH_4Cl); two P treatments (0.025 mg PO_4-P/L or 0.25 mg PO_4-P/L as NaH_2PO_4); and three treatments in which we altered the N:P ratio (low [1:2.5], medium [4:1], and high [40:1]). Randomization was accomplished using the design-of-experiments routines within S-Plus for Windows, version 3.3 (MathSoft, Seattle, Washington, USA). N concentrations were chosen to bracket measured rates of annual deposition. P concentrations were also varied to determine whether plants responded to N limitation directly or to P limitation caused by increased N availability (Bedford et al. 1999).

At the start of the experiment, we removed from each plant all pitchers that had been produced in previous years. Although pitchers of *S. purpurea* persist for up to two years following their production, pitchers that survive through a winter rarely capture prey or support inquilines (Fish and Hall 1978), and their photosynthetic rate is less than 5% that of a new pitcher (A. M. Ellison, *unpublished data*). We have seen no evidence that removing old or senescent pitchers affects subsequent plant growth. As each new leaf opened on a plant, any pitcher liquid was removed and replaced by the assigned nutrient concentration. Leaves were plugged with glass wool to prevent prey capture and colonization by inquilines. Every two weeks, we removed the water from all the pitchers of a plant and reapplied the treatment. No evidence of nitrogen burning was observed throughout the experiment.

There is no evidence that manipulating water or nutrient levels per se introduced an experimental artifact. In any given season, water levels within pitchers varies, but except in very dry years, there is always some water present (Kingsolver 1981). At both Hawley and Molly Bogs, there is normally 5–20 mL of water in the pitcher at any given time (A. M. Ellison and N. J. Gotelli, *unpublished data*). Nutrient concentrations also vary over time, ranging from 0 to 1.3 mg NH_4-N/L and 0 to 0.27 mg PO_4-P/L over the course of a growing season (A. M. Ellison, N. J. Gotelli, and L. A. Bledzki, *unpublished data*). Rainfall and prey are the dominant sources of nutrients for *S. purpurea* (Bledzki and Ellison 1998). Because of its poorly developed root system, *S. purpurea* derives <5% of its nutrients from the pore water in the peat where it grows (Bledzki and Ellison 1998, 2001).

Treatments were established in the spring of 1998 and maintained through the 1998 and 1999 field seasons. At the end of each summer, we recorded the size, survivorship, and reproductive status of all plants.

TABLE 1. Stage transition matrix for *Sarracenia purpurea* populations at Hawley Bog, Massachusetts (USA) and Molly Bog, Vermont (USA).

Stage at year $t + 1$	Stage at year t			
	Recruit	Juvenile	Non-flowering adult	Flowering adult
Recruit				
Hawley Bog	0.0000	0.0000	0.0000	4.0000
Molly Bog	0.0000	0.0000	0.0000	4.0000
Juvenile				
Hawley Bog	0.1000	0.9540	0.0900	0.0000
Molly Bog	0.1000	0.8540	0.1770	0.0000
Non-flowering adult				
Hawley Bog	0.0000	0.0360	0.7010	0.8375
Molly Bog	0.0000	0.1310	0.7080	0.6660
Flowering adult				
Hawley Bog	0.0000	0.0000	0.1802	0.1610
Molly Bog	0.0000	0.0000	0.1000	0.3070

Stage-based matrix model

We constructed a matrix model of population growth in which individuals were classified into four discrete stages: recruits, juveniles, non-flowering adults, and flowering adults (Brewer 2001). The time step of the model was one year, so the transition from flowering adult to recruit incorporated fruiting, seed set, recruitment, and early juvenile mortality. The model is

$$\mathbf{n}(t + 1) = \mathbf{An}(t) \quad (1)$$

where $\mathbf{n}(t)$ is the vector of the number of plants in each stage at time t, and $\mathbf{A}$ is the 4×4 transition matrix (Caswell 2001). After an initial transient series of 1000 time steps, we estimated the intrinsic rate of increase (r) as $\ln(N(t + 1)/N(t))$ where $N(t)$ is the total population size forecast by the model at time t. The initial stage vector was 100 plants in each of the four stages. We wrote a computer program in Delphi 5.0 to iterate Eq. 1 and to calculate demographic parameters for the different simulation models.

LTRE models

For each nutrient treatment, we constructed a stage transition matrix by averaging the estimated transitions from the two consecutive years of the experiment. We did not count seeds produced by plants in this experiment. Rather, we assumed that the recruitment transitions in all treatments were equivalent to those measured in the demographic survey (Table 1); all other transitions were derived from the experimental data. For each nutrient treatment, we first estimated r using a deterministic model. Next, we estimated r using a stochastic model in which the annual variation in rates represented measurement error. Treating the variation as measurement error is appropriate because the nutrient treatments were being maintained as an ecological "press" experiment (Bender et al. 1984). We tested

the statistical significance of variation in r among treatments with a form of life-stage simulation analysis (Wisdom et al. 2000). We created a set of 1000 transition matrices for each experimental treatment, iterated each matrix to estimate r, and calculated variances and confidence intervals.

Forecasting model for N-deposition scenarios

Although the LTRE models provide insight into the equilibrium dynamics for populations in different N regimes, these models are not realistic for forecasting purposes. In the real world, N deposition changes gradually over long time periods, and fluctuates substantially in the short run. What are population dynamics under such conditions?

To answer this question, we used long-term data from the National Atmospheric Deposition Program (NADP 2000) to forecast trends in annual N deposition rates. Time series for NH_4 and NO_3 were available from 1984–1998 from monitoring stations at Quabbin, Massachusetts (USA) (~50 km southeast of Hawley Bog) and Shelburne, Vermont (USA) (~60 km northwest of Molly Bog). Additional data (Ellison and Gotelli 2002) illustrate that deposition rates at Quabbin and Shelburne are within 10% of those at Hawley and Molly Bogs, respectively. We combined concentration data (in milligrams per liter per year) for NH_4 and NO_3 to generate a single time series of annual N deposition at each site. Next, we fit a first-order autoregressive model with correlated errors (AR-1) to forecast long-term N deposition:

$$N_t = a + bN_{t-1} + e \quad (2)$$

where N_t is the nitrogen deposition rate in year t, e is a random error term, and a and b are fitted constants. In our models, we set $a = 0$, to describe a constant percentage increase or decrease in annual deposition rates.

We used this model to forecast N deposition under four scenarios: (1) best fit (continuing the annual 4.7% or 2.2% decreases of the fitted models for Massachusetts and Vermont, respectively); (2) no change (assuming current N levels measured at each site in 1998, and then using the error structure of the model to forecast into the future); (3) small (1%) annual increase in N; (4) large (2.2% or 4.7%) annual increase in N.

For comparison, we also fit nitrogen time series with an ordinary least-squares (OLS) model, which does not assume correlated errors:

$$N_t = a + bt + e. \quad (3)$$

Error terms (e) were fitted separately for the AR-1 and OLS models. Nitrogen forecasting models were fit using SYSTAT 6.0 (Wilkinson 1996).

Next, we used the experimental data from the control, low-N, and high-N treatments to create an N function for each transition in the matrix model. This function takes the N deposition rate as input and generates
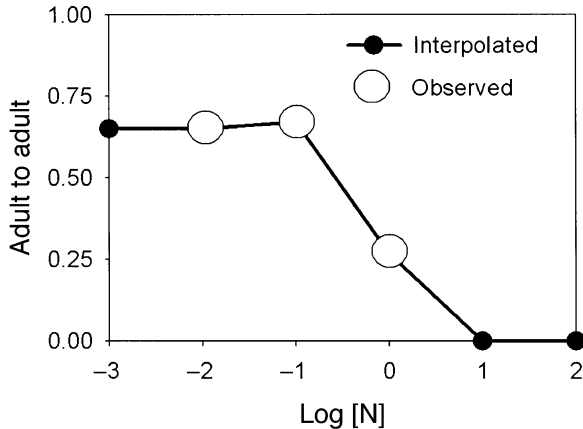
FIG. 1. Sample calculation of transition functions for the nonstationary population growth model. The *x*-axis is the $\log_{10}$ concentration of nitrogen. The *y*-axis is the persistence transition for adult plants (probability that a nonflowering adult plant persists as a nonflowering adult plant from one year to the next). The three open circles are the observed experimental values from the nutrient-addition experiment. The solid circles and solid line are the interpolated values for unobserved transition probabilities.

the transition probabilities for the matrix model as output. We used the results from the nutrient-addition experiment to model transition matrices in different nitrogen environments. The function takes as inputs the current N concentration and produces as output the transition probabilities for each element in the transition matrix. To estimate the function, we assumed: (1) that at concentrations ≤ 0.01 mg·L^{-1}·yr^{-1}, the transition probability equals that observed for the control plants; (2) that at concentrations ≥ 10 mg·L^{-1}·yr^{-1} (10 times our high-N treatment), all plants are killed (transition probability = 0.0); (3) between these extremes, transition probabilities are determined by a simple linear interpolation between our experimental data points plotted on a logarithmic scale of N concentration (Fig. 1).

Finally, we used the N forecasting equations to generate a random series of annual deposition environments, created the sequential transition matrices from these, and used this series of matrices to forecast population dynamics. We forecast N deposition by extrapolating the N forecasting equations for 1000 consecutive time steps. We then used the transition functions to establish 1000 sequential transition matrices, each determined by the N concentrations in a particular year. Finally, we applied those sequential matrices to an initial population vector to forecast population dynamics.

Because the transition matrices change systematically at each time step, the system is non-homogenous and never reaches an equilibrium (Caswell 2001). Thus, *r* is not meaningful in this nonstationary model. However, it is appropriate to estimate the probability of extinction and the time to extinction (Sjögren-Gulve and Ebenhard 2000). These extinction estimates may

be contingent on the initial population size and distribution of individuals among stages (Tuljapurkar 1990).

To determine reliable starting population sizes for the model, we estimated total population sizes of *S. purpurea* at Hawley and Molly Bogs. At each bog, we measured plant size and density in two randomly located 5×5 m plots. Additional data on seed dispersal suggests that the distribution of plants in these plots is representative of the distribution of plants at each site (Ellison and Parker 2002). We estimated the area of the bog mat at each bog from U.S. Geological Survey aerial photographs, and simply multiplied the density of juveniles and adults in our sample plots by bog mat area to get an estimator for initial population sizes. We ran the model 1000 times to estimate the probability of extinction after 100 yr (the fraction of populations that declined below 1.0 individual after one century). We defined the time to extinction as the number of time steps for which 95% of the populations had declined below 1.0 individual. This is a low and conservative extinction threshold (Ginzburg et al. 1982), but it may be a realistic one for long-lived perennial plants, which can persist at very small population sizes for extended periods.

RESULTS

Demographic projections

The projection model based on the average annual demographic rates (Table 1) indicates a close balance between fecundity and mortality schedules at each site. The measured rate of intrinsic increase was $r = 0.00456$ individuals per individual per year at Hawley Bog (Massachusetts, USA), and 0.00554 ind.·ind.$^{-1}$·yr^{-1} at Molly Bog (Vermont, USA). Corresponding doubling times were 152 yr and 125 yr, respectively. Simple stochastic models (not shown) generated similar results, with 95% confidence intervals that bracketed 0.0.

Nutrient-addition experiment and LTRE model

In this deterministic LTRE model, the measured rates of population increase differed among the nine experimental treatments (Fig. 2A). The highest rates were measured for the controls and the P-addition treatments. The lowest rates were measured for the high-N treatment and the high N:P-ratio treatments. A stochastic model that incorporated measurement error generated similar patterns, although variances were large because transitions were estimated with only 10 plants per size class in each experimental treatment (Fig. 2B). In the stochastic model, the probability of extinction after 100 yr was substantially higher for the high-N and the high N:P-ratio treatments.

Nitrogen forecasting models

The autoregressive model described a decrease in N concentration over the 14-yr time series (1984–1998), with an estimated decrease of 4.7% annually (b =
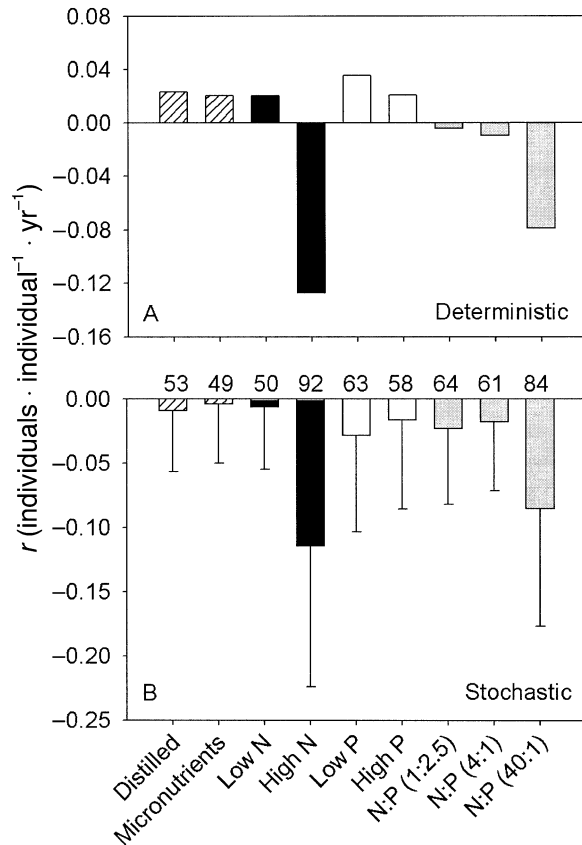
FIG. 2. Estimated r (intrinsic rate of increase) for *Sarracenia purpurea* populations in different nutrient treatments. Hatched bars = controls; solid bars = nitrogen treatments; open bars = phosphorus treatments; gray bars = N:P ratio treatments (manipulated ratios indicated in parentheses). (A) Deterministic-model results. The deterministic model was calculated using a single transition matrix derived for each treatment in the nutrient-addition experiment. (B) Stochastic-model results. The stochastic model assumes that between-year variation in observed matrix transitions was due entirely to measurement error. The bar indicates the median r for 1000 simulated populations for each model, and the line indicates 1 SD. The number above each bar is the percentage of simulated populations that went extinct (simulated population size <1.0) within 100 yr.

0.953, σ of e = 0.042 in Eq. 2) at the Quabbin, Massachusetts (USA) monitoring station and 2.2% annually at the Shelburne, Vermont (USA) one (b = 0.979, σ of e = 0.158). The linear models described an annual decrease of b = −0.004 mg/L (σ of e = 0.075 in Eq. 3) at Quabbin and b = −0.001 mg/L (σ of e = 0.065) at Shelburne.

A population forecasting model with continued decrease in annual N deposition predicted virtually no extinction risk for *S. purpurea* at Hawley Bog during the next century. A model of no change from the 1998 N deposition rates predicted only a small extinction risk (P = 0.038), whereas even a 1% increase in the annual deposition rate generated a substantial extinction risk (P = 0.378). The expected time to extinction ranged from 70 to 650 yr (Table 2). However, regardless of the expected extinction time, all forecasting scenarios except for the best-fit model predicted steady decreases in the size of the *S. purpurea* population.

For all N-deposition scenarios, extinction risks were higher at Molly Bog than at Hawley Bog (Table 2), reflecting the higher initial deposition rate and lower forecast rate of N decline at the Shelburne vs. the Quabbin monitoring stations. Even the scenario of long-term decline in annual deposition at Molly Bog still resulted in a substantial risk of extinction after 100 yr (P = 0.158).

There were also differences in population trajectories derived from linear vs. autoregressive N-deposition time series. Runs of the linear models exhibited much less variability, and did not cross the extinction threshold before 100 yr (Table 2). The linear models usually forecast a simple exponential increase or decrease in population size, whereas the autoregressive models often generated periodic fluctuations (Fig. 3).

DISCUSSION

Increased N deposition has been implicated in the extinction of several *Sphagnum* species in upland areas of northern England (Press et al. 1986), and in a shift from *Calluna*-dominated heathland to grassland in the Netherlands (Heil and Diemont 1983). Although studies of N saturation have mostly emphasized ecosystem function and individual plant responses, these responses are ultimately linked to the persistence of populations (Doak and Morris 1999). A detrimental feedback loop may emerge, in which increased N deposition causes the species' extinction, and a consequent loss of the system's capacity to absorb excess N (Reich et al. 2001, Symstad and Tilman 2001).

Simple deterministic and stochastic models of field census data suggest that mortality and birth schedules of *Sarracenia purpurea* at Hawley and Molly Bogs (New England, USA) are in close balance, a pattern often observed for perennial plants (Caswell 1986, Silvertown et al. 1993). Population growth rates are sensitive to N and P additions and population declines can be expected with high N and high N:P ratios (Fig. 2). Our forecasting model suggests that the risk of extinction after 100 yr is small under current or declining deposition rates, but that even small increases generate substantial extinction risks (Table 2). However, extinction times are on the order of decades to centuries, and short-term increases in population size may be superimposed on long-term decreases (Fig. 3). Such fluctuations are usually thought to characterize density-dependent models with a time lag (May 1974, Tilman and Wedin 1991), or models with exogenous environmental drivers (Turchin and Taylor 1992, Ellner and Turchin 1995). Our analyses suggest that these fluctuations can also arise in simple stage-structured models with temporal autocorrelations in demographic rates. Without a long-term forecasting model and a pro-

TABLE 2. Extinction risks and times to extinction of *Sarracenia purpurea* populations under different scenarios of annual nitrogen (N) deposition.

	Autoregressive model, Eq. 2			OLS (linear) model, Eq. 3		
Scenario	Annual change in N (%)	Prob.$_{ext.}$ at 100 yr†	Time to ext. (yr)‡	Coefficient, OLS§	Prob.$_{ext.}$ at 100 yr†	Time to ext. (yr)‡
Hawley Bog						
Best case	−4.7	0.000	>10 000	−0.004	0.000	>10 000
No change	0.0	0.038	650	0.000	0.000	220
Small increase	1.0	0.378	290	0.001	0.000	180
Worst case	4.7	0.996	70	0.004	0.000	140
Molly Bog						
Best case	−2.2	0.158	>10 000	−0.001	0.000	250
No change	0.0	0.510	230	0.000	0.000	180
Small increase	1.0	0.694	200	0.0005	0.000	160
Worst case	2.2	0.838	140	0.001	0.000	150

Notes: Model coefficients were derived for Hawley Bog from the Quabbin, Massachusetts (USA) National Atmospheric Deposition Program (NADP 2000) N time series, and for Molly Bog from the NADP Shelburne, Vermont, N time series. For Hawley Bog, the initial N deposition rates in the model were 0.391 mg·L^{-1}·yr^{-1}, and, for Molly Bog, 0.477 mg·L^{-1}·yr^{-1} (NADP measured levels in 1998).

† Probability of extinction is defined as the fraction of 1000 random population time series that had gone extinct (total population size <1.0) by 100 years.

‡ Time to extinction is the length of the time series required for 950 out of 1000 random population time series to fall below the extinction threshold of 1.0 individuals.

§ OLS = ordinary least-squares model, Eq. 3.

spective analysis (Caswell 2000), it may be difficult to recognize the potential risk of extinction for slow-growing populations.

Our model does have some limitations. First, it does not include any density dependence—transition probabilities are not affected by current population size (Grant and Benton 2000). However, *S. purpurea* densities in ombrotrophic bogs of New England are typically low, and so far there is no evidence for simple density dependence from field manipulations of *Sarracenia* (Ellison et al., *in press*). Our model also does not include any spatial dynamics (Horvitz and Schemske 1995). However, the demography of cohorts growing in different bog microhabitats did not differ substantially (N. J. Gotelli and A. M. Ellison, *unpublished data*). Because the plant cohort was chosen from a relatively high-density area in the center of the bog, demographic estimates could be different for plants that were randomly selected because there appears to be little recruitment of juveniles near the edges of the bog. However, plant densities in these outlying areas are very low, so they may not contribute much to population dynamics. Although our model does not incorporate explicit terms for covariance among demographic rates (Benton and Grant 1996), covariance structure is present because of the correlated responses of each transition element to different N regimes. Finally, we have not incorporated interactions of *S. purpurea* with other plant species that may be responding to changes in nitrogen (Brewer 2001). In other field experiments, we are examining interactions with inquilines and prey, and their contributions to the plant's N budget (A. M. Ellison and N. J. Gotelli, *unpublished data*). However,

the net effects of inquiline activity may be small compared to anthropogenic inputs of N (Chapin and Pastor 1995, Bledzki and Ellison 1998).

Although the NADP time series from 1984 through 1998 generated an optimistic prediction of decreased deposition rates (see Krajick 2001), substantial increases in N deposition are expected in the long term (Tilman et al. 2001). The models presented here indicate the time frame for population responses under such sce-
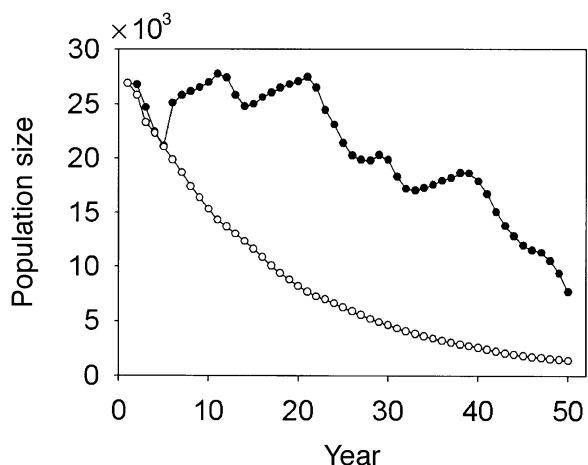

FIG. 3. Predicted population trajectories for *Sarracenia purpurea* population at Molly Bog (Vermont, USA) using autoregressive (solid circles) and ordinary least-squares (open circles) models for forecasting nitrogen deposition series. For the autoregressive model (Eq. 2), the N time series is modeled with the best-fit coefficients $a = 0.0$, $b = 0.978$. For the ordinary least-squares model (Eq. 3), the best-fit coefficients were $a = 0.477$ and $b = -0.001$.

narios and could be used as a starting point for developing effective strategies to conserve plant populations (Finn et al. 1998, Ferson and Burgman 2000). Forecasting extinction risk in long-lived organisms is inherently challenging, and requires a strong modeling component (e.g., Fujiwara and Caswell 2001). The approach we advocate here is to build a simple forecasting model that incorporates short-term measurements of demographic rates, results of manipulative field experiments, and long-term monitoring records of environmental change.

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