Ecology, 83(10), 2002, pp. 2758–2765

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

NICHOLAS J. GOTELLI[1,3] AND AARON M. ELLISON[2,4]

[1]*Department of Biology, University of Vermont, Burlington, Vermont 05405 USA*
[2]*Department of Biological Sciences, Mount Holyoke College, South Hadley, Massachusetts 01075 USA*

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;

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 ev-

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

Stage at year t 1 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

$$\mathbf{n}(t\ 1\ 1)\ 5\ \mathbf{An}(t) \qquad (1)$$

where $\mathbf{n}(t)$ is the vector of the number of plants in each stage at time t, and $\mathbf{A}$ is the 4 3 4 transition matrix (Caswell 2001). After an initial transient series of 1000 time steps, we estimated the intrinsic rate of increase (r) as $\ln(N(t\ 1\ 1)/N(t))$ 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

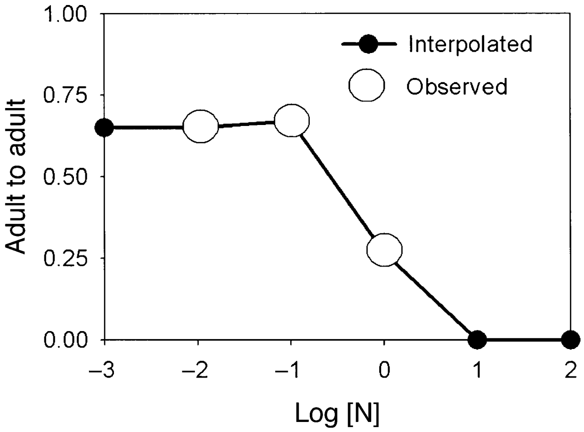

FIG. 1. Sample calculation of transition functions for the nonstationary population growth model. The *x*-axis is the $\log_{10}$ concentration of nitrogen. The *y*-axis is the persistence transition for adult plants (probability that a nonflowering adult plant persists as a nonflowering adult plant 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 $\leq$0.01 mg·L^{21}·yr^{21}, the transition probability equals that observed for the control plants; (2) that at concentrations $\geq$10 mg·L^{21}·yr^{21} (10 times our high-N treatment), all plants are killed (transition probability 5 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 3 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* 5 0.00456 individuals per individual per year at Hawley Bog (Massachusetts, USA), and 0.00554 ind.·$ind.^{21}$·yr^{21} 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

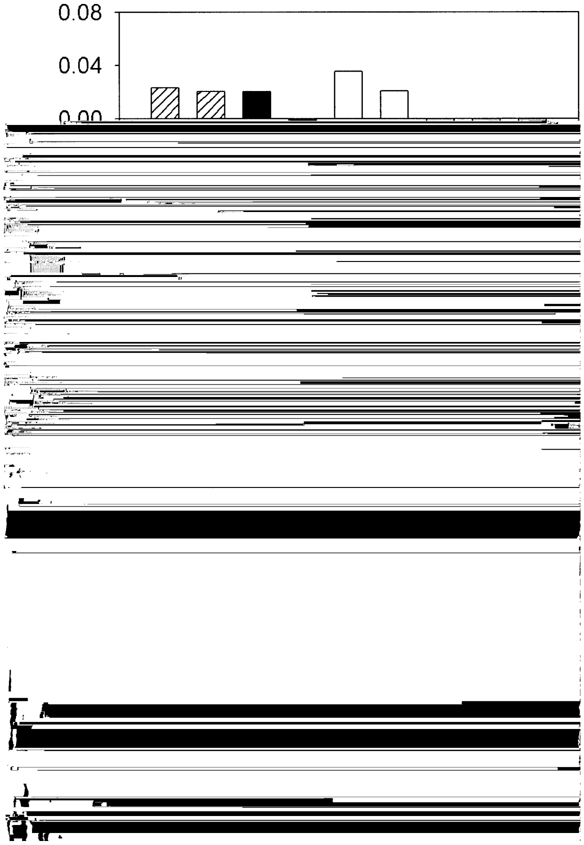

FIG. 2. Estimated *r* (intrinsic rate of increase) for *Sarracenia purpurea* populations in different nutrient treatments. Hatched bars 5 controls; solid bars 5 nitrogen treatments; open bars 5 phosphorus treatments; gray bars 5 N:P ratio treatments (manipulated ratios indicated in parentheses). (A) 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, s of *e* 5 0.042 in Eq. 2) at the Quabbin, Massachusetts (USA) monitoring station and 2.2% annually at the Shelburne, Vermont (USA) one (*b* 5 0.979, s of *e* 5 0.158). The linear models described an annual decrease of *b* 5 20.004 mg/L (s of *e* 5 0.075 in Eq. 3) at Quabbin and *b* 5 20.001 mg/L (s of *e* 5 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* 5 0.038), whereas even a 1% increase in the annual deposition rate generated a substantial extinction risk (*P* 5 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* 5 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 thresh-

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

Scenario	Autoregressive model, Eq. 2			OLS (linear) model, Eq. 3		
	Annual change in N (%)	Prob.$_{\text{ext.}}$ at 100 yr†	Time to ext. (yr)‡	Coefficient, OLS§	Prob.$_{\text{ext.}}$ at 100 yr†	Time to ext. (yr)‡
Hawley Bog						
Best case	24.7	0.000	. 10 000	20.004	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	22.2	0.158	. 10 000	20.001	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^{21}·yr^{21}, and, for Molly Bog, 0.477 mg·L^{21}·yr^{21} (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 5 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-

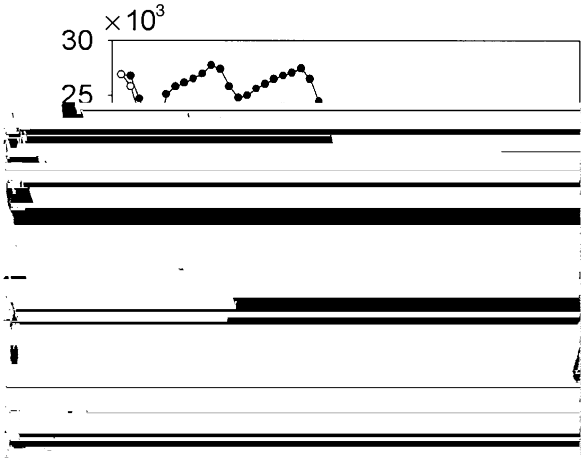

FIG. 3. Predicted population trajectories for *Sarracenia purpurea* population at Molly Bog (Vermont, USA) using autoregressive (solid circles) and ordinary least-squares (open circles) models for forecasting nitrogen deposition series. For the autoregressive model (Eq. 2), the N time series is modeled with the best-fit coefficients *a* 5 0.0, *b* 5 0.978. For the ordinary least-squares model (Eq. 3), the best-fit coefficients were *a* 5 0.477 and *b* 5 20.001.

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.

ACKNOWLEDGMENTS

We thank our hard-working field crew (H. Albright, L. Bledzki, R. Emerson, K. Matthews, K. McKnight, J. Sears, S. Schachterle, and M. Toomey) for assistance in monitoring plants and maintaining experiments. The manuscript benefited from comments by Alison Brody, Cathy Pfister, Anne Worley, and the University of Vermont Ecology Discussion Group. Research supported by NSF grants 98-05702 and 98-08504 to A. M. Ellison and N. J. Gotelli. Computer modeling supported by NSF grants DBI 97-25930 and DEB 01-07403 to N. J. Gotelli.

LITERATURE CITED

Aber, J. D., A. Magill, K. J. Nadelhoffer, R. Boone, J. Melillo, P. Steudler, J. Hendricks, R. Bowden, W. Currie, and W. McDowell. *In press*. The chronic nitrogen experiment. *In* D. R. Foster and J. D. Aber, editors. Forest landscape dynamics in New England: ecosystem structure and function as a consequence of history. Yale University Press, New Haven, Connecticut, USA.

Aber, J. D., W. H. McDowell, K. J. Nadelhoffer, A. H. Magill, G. Berntson, M. Kamekea, S. G. McNulty, W. Currie, L. Rustad, and I. Fernandez. 1998. Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. BioScience **48**:921–934.

Addicott, J. F. 1974. Predation and prey community structure, an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. Ecology **55**: 475–492.

Bedford, B. L., M. R. Walbridge, and A. Aldous. 1999. Patterns of nutrient availability and plant diversity of temperate North American wetlands. Ecology **80**:2151–2169.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology **65** density-dependent populations in stochastic environments. Ecology **81**:680–693.

Heard, S. B. 1994. Pitcher-plant midges and mosquitoes, a processing chain commensalism. Ecology **75**:1647–1660.

Heil, G. W., and W. M. Diemont. 1983. Raised nutrient levels change heathland into grassland. Vegetatio **53**:113–120.

Hemond, H. F. 1983. The nitrogen budget of Thoreau's Bog. Ecology **64**:99–109.

Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecological Monographs **65**:155–192.

Juniper, B. E., R. B. Robins, and D. M. Joel. 1989. The carnivorous plants. Academic Press, London, UK.

Kearsley, J. 1999. Non-forested acidic peatlands of Massachusetts: a statewide inventory and vegetation classification. Massachusetts Natural Heritage and Endangered Species Program, Westborough, Massachusetts, USA.

Kingsolver, J. G. 1981. The effect of environmental uncertainty on morphological design and fluid balance in *Sarracenia purpurea* L. Oecologia **48**:364–370.

Krajick, K. 2001. Long-term data show lingering effects from acid rain. Science **292**:195–196.

May, R. M. 1974. Biological populations with non-overlapping generations: stable points, stable cycles, and chaos. Science **186**:645–647.

Menges, E. 1992. Stochastic modeling of extinction in plant populations. Pages 253–275 *in* P. L. Fiedler and S. K. Jain, editors. Conservation biology: the theory and practice of nature, conservation, preservation and management. Chapman and Hall, New York, New York, USA.

Moizuk, G. A., and R. B. Livingston. 1966. Ecology of red maple (*Acer rubrum* L.) in a Massachusetts upland bog. Ecology **47**:942–950.

NADP 2000. National Atmospheric Deposition Program. [Online, URL: ^http://nadp.sws.uiuc.edu&.]

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature **368**