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0030-0950/83/0001-0019 \$2.00/0

POPULATION GROWTH OF THE PITCHER PLANT, *SARRACENIA PURPUREA* L., AT CRANBERRY BOG, LICKING COUNTY, OHIO¹

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ABSTRACT. A population of the pitcher plant, *Sarracenia purpurea* L., at Cranberry Bog Nature Preserve, Licking County, Ohio, was founded by a single individual transplanted to the bog in 1912. From an observation of the population in 1921, the intrinsic rate of increase for this population was estimated to be between .0016 and .0023 per day. A recent survey of the present size of the population revealed approximately 157,000 pitcher plants. These observations suggest that the population has not only reached the carrying capacity of Cranberry Bog, but that it did so as early as 1942. Comparisons between the intrinsic rate of increase for *S. purpurea* and the few other plant species that have been studied suggest that pitcher plants have a relatively slow rate of population increase for an herbaceous species.

OHIO J. SCI. 83 (1): 19-22, 1983

INTRODUCTION

Despite the importance of population growth to an understanding of the ecology and evolution of plant populations, few studies have presented reliable estimates of the growth rates of plant populations in nature. The few estimates that do exist

have been arrived at through demographic studies of age-specific birth and death rates which sample population growth rates during only a short period of a population's history.

A unique opportunity to directly monitor population growth over an extended period has arisen from an unusual historical event. The population of pitcher plants, *Sarracenia purpurea* L., at Cranberry Bog

¹Manuscript received 28 May 1981 and in revised form 25 September 1981 (#81-22).

Nature Preserve, Licking County, Ohio, was founded by a single individual plant brought to the bog in 1912 by Freda Detmers, graduate student in botany at The Ohio State University (Schaffner 1922). The population was observed by Schaffner in 1921 to consist of hundreds of individuals, and today pitcher plants cover the bog.

Sarracenia purpurea L. (Sarraceniaceae) is an insectivorous, herbaceous perennial found in low nutrient, usually bog soils along the eastern coast of the United States and west to British Columbia (Crow 1969). It was reported to have existed in several Ohio bogs before their destruction. Unlike pitcher plant sites originating through natural processes, Cranberry Bog was accidentally created with the construction of Buckeye Lake in 1832. Consequently, pitcher plants did not grow there until their introduction in 1912. Despite some vegetative propagation by rhizomes (personal observation), most new plants appear to develop from the small seeds (2 mm) and probably spend several years in a juvenile period of vegetative growth. A flowering plant may produce 10,000 seeds in one year, indicating a very high potential for population growth. A 6-week period of stratification followed by warm temperatures results in nearly 100% germination in the laboratory. These observations suggest high rates of mortality before and during seedling establishment. The continuous blanketing growth of the sphagnum may account for much of this mortality. The effects of the genetic bottleneck resulting from the founding event of *S. purpurea* at Cranberry Bog has been examined in another paper (Schwaegerle and Schaal 1979).

POPULATION GROWTH RATES

An estimate of the intrinsic rate of increase for the first 9 years of population growth at Cranberry Bog can be based upon Shaffner's (1922) observation. The Lotka model of exponential population growth, $N_t = N_0 e^{rt}$, states that the number of individuals in a population at any

time (N_t) is a function of the number at time zero (N_0), time (t), and the intrinsic rate of increase (r). Such an estimate will only be accurate for a population during a period of exponential growth. Density-dependent, rate limiting factors which would cause deviation from exponential increase can be assumed to be negligible during the first years of colonization. Interpreting Shaffner's words "hundreds of vigorous plants" conservatively as 200 plants, results in an average intrinsic rate of increase of .0016 per day for this period of the population's history. A generous interpretation of 2000 individuals modifies the estimate of r only slightly (.0023 per day). The intrinsic rate of increase for *S. purpurea* at Cranberry Bog almost certainly lies between these 2 values.

Since a 67-year period of population growth at this rate would produce an unrealistically large number of plants for the limited area of Cranberry Bog, an estimate of current population size (1978) becomes interesting. Such an estimate was obtained by sampling the bog with a 0.50 m² frame. Fifty casts of the square at regular intervals along 2 transects of the population approximates a random sample of plant density. A mean density of 6.12 ± 1.00 SE individuals per 0.50 m² was calculated using this procedure. The area of the bog was estimated from measurements obtained with a Silva range finder to be approximately 12,000 m². The 95% confidence interval for population size is $157,000 \pm 50,000$ individuals.

From the above minimum and maximum estimates of intrinsic rate of increase (.0016 and .0023) and population size, the carrying capacity for *S. purpurea* at Cranberry Bog can be calculated. Population growth can be examined using Verhulst's logistic model of population growth, $dN/dt = rN(1-N/K)$, where K represents the carrying capacity of the environment. The number of individuals in a population at time t is expressed by:

$$N_t = \frac{K}{1 + [(K - N_0)/N_0]e^{-rt}}$$

Substituting either the minimum or the maximum estimate of r in the equation, results in a value for K equal to present population size, 157,000. Since population size would be expected to be fairly constant at Cranberry Bog due to the slow growth and longevity of established plants, this is probably a good estimate of the carrying capacity of the bog. The logistic growth model with the minimum estimate of r of .0016 also suggests that population numbers approached their present level as early as 1942. This unique situation offers an excellent opportunity to study the demographic processes in plant populations which result in density-dependent limits to growth.

Estimates of the intrinsic rate of increase for populations of other plant species (table 1) demonstrate that the estimate derived for *S. purpurea* is a reasonable one. However, this value falls towards the lower end of the growth rates exhibited by the herbaceous species that have been studied. A low intrinsic rate of increase in the pitcher plant would be consistent with several other life history features such as: 1) populations at the carrying capacity of available habitat, 2) infrequent opportunities for colonization of new habitat, and 3) high interspecific competition in the predictable, fairly constant environment

TABLE 1

Maximum intrinsic rates of increase observed in field populations of 8 plant species (Leverich and Levin 1979, Werner and Caswell 1977, Sarukhan and Gadgil 1974, Hartshorn 1972, 1975).

Species	Habit	Maximum observed r
<i>Phlox drummondii</i>	annual herb	.0024/day
<i>Dipsacus sylvestris</i>	biennial herb	.0026
<i>Ranunculus repens</i>	perennial herb	.0016
<i>R. bulbosus</i>	perennial herb	.0058
<i>R. acris</i>	perennial herb	.0023
<i>Sarracenia purpurea</i>	perennial herb	.0016-.0023
<i>Pentaclethra maculosa</i>	tropical tree	.0001
<i>Stryphnodendron excelsum</i>	tropical tree	<.0001

a bog offers. The doubling time for the population during the early colonization period is 1.2 and .82 years for the minimum and maximum estimate of r , respectively.

In contrast to the scarcity of information on plant populations, many estimates of r for animal species are available. Animals exhibit a wider range of values and often much higher rates of increase than plants. For example, the beetle, *Tribolium confusum*, at optimal conditions has an intrinsic rate of increase of .120 per day, while *Homo sapiens* has an r of .0003 per day (Pianka 1974). Pitcher plants fall toward the lower end of this continuum.

In conclusion, Cranberry Bog appears to have been a favorable environment for the pitcher plant. The observations discussed here suggest the population expanded throughout the bog and probably saturated the habitat after about 30 years. *Sarracenia purpurea* has an intrinsic rate of increase in agreement with other herbaceous species that have been studied. That *S. purpurea* falls in the lower end of these values is consistent with other features of its life history which suggest a generally more K -selected strategy than might be expected for an herbaceous plant. The great number of pitcher plants at Cranberry Bog reflects the impact of exponential growth in an open environment and suggests that even non-weedy plant populations can respond surprisingly rapidly to new resources.

ACKNOWLEDGMENTS. The author thanks Barbara A. Schaal, Barbara L. Benner, the 2 anonymous reviewers, and the members of the Gleason Memorial Plant Ecology Laboratory at the University of Illinois for their support and helpful suggestions in the preparation of this manuscript. This study was supported by a Sigma Xi Grant-In-Aid and by NSF grant DEB 76-09709.

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