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BRIEF COMMUNICATION

SEED DISPERSAL AND SEEDLING ESTABLISHMENT OF *SARRACENIA PURPUREA* (SARRACENIACEAE)[1]

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Plant ecologists continue to grapple with Reid's paradox, the observation that dispersal distances of most herbs and trees are too limited to account for their recolonization of northern latitudes following glacial recession. As global climate changes and natural habitats become increasingly fragmented, understanding patterns of seed dispersal and the potential for long-distance colonization takes on new importance. We studied the dispersal and establishment of the northern pitcher plant *Sarracenia purpurea*, which grows commonly in isolated bogs throughout Canada and eastern North America. Median dispersal distance of *S. purpurea* is only 5 cm, which is insufficient to explain its occurrence throughout formerly glaciated regions of North America. Establishment probability of seeds in the field is approximately 5%, and juveniles are normally found clustered around adult plants. The large-scale population genetic structure of this species can be accounted for by rare long-distance dispersal events, but its predictable occurrence in isolated habitats requires additional explanation. Reid's paradox remains an open question, and predicting long-range colonization into fragmented habitats by species with limited dispersal ability is a novel challenge.

Key words: dispersal; establishment; germination; Reid's paradox; *Sarracenia purpurea*; Sarraceniaceae.

Dispersal and establishment are central features of plant life history, yet far less is known about them than about later stages of plant growth and reproduction. Since the end of the 19th century, plant biologists have been perplexed by the observation that mean and maximum dispersal distances of most herbs and trees are insufficient to explain their recolonization of northern latitudes following glacial recession (Reid, 1899). This observation, termed ''Reid's paradox'' (Clark et al., 1998), has received renewed attention because global climate change and habitat fragmentation present new challenges for plant dispersal and colonization of new habitats (Cain, Damman, and Muir, 1998; Higgins and Richardson, 1999; Nathan and Muller-Landau, 2000; Cain, Milligan, and Strand, 2000; Pakeman, 2001). Although Reid's paradox essentially has been solved for trees (e.g., Clark, 1998; Higgins and Richardson, 1999), it remains an open question for herbs.

Plants that occur in naturally isolated habitats present additional challenges for models of seed dispersal (Clark, 1998; Higgins and Richardson, 1999; Pakeman, 2001). These models implicitly assume that long-distance dispersers can cross habitat boundaries unimpeded or that at least all habitat between the source population and the furthest colonizing site is suitable for establishment. For many habitats, this is not the case, as increasing urbanization and other landscape transformations render intervening habitat unsuitable either for establishment or for disperser stopovers.

In northeastern North America, *Sphagnum* bogs occur as isolated wetlands, usually surrounded by forests and fields. Even large expanses of bogs are being fragmented by peat mining and afforestation (Pellerin and Lavoie, 2000). Many plants that grow in bogs are habitat specialists, yet they have broad geographic ranges. Colonization of these habitats had to have occurred by crossing large expanses of nonwetlands (forests, grasslands, etc.) in which wetland plants cannot survive. Thus, understanding dispersal and establishment dynamics of bog plants may provide additional insights into models for the migration dynamics of plants as our climate changes rapidly. In this paper, we describe the dispersal and seedling establishment of the northern pitcher plant, *Sarracenia purpurea* L. subsp. *purpurea* (Raf.) Wherry, a common plant in bogs throughout Canada and the northeastern United States (Schnell, 1979). This subspecies ranges from Maryland northward, but the entire species (including the three varieties of subsp. *venosa* [Raf.] Wherry) ranges from Florida to Newfoundland on the eastern coast of North America and westward across Canada (Schnell, 1979). The single-flowered inflorescence of *S. purpurea* blooms in late May to early June. Capsules mature over the summer and dehisce in late fall, releasing 500–1500 seeds each. Its seeds are small (1.8–2.4 mm in length) and unornamented and have nondeep morphophysiological dormancy (Ellison, 2001). Field work for this study was conducted at Hawley Bog, an approximately 3-ha ombrotrophic stream headwaters bog in northwestern Massachusetts, USA (Moizuk and Livingston, 1966). *Sarracenia purpurea* seeds are not found in the persistent seed bank at Hawley Bog (A. M. Ellison and H. R. Steinhoff, Mount Holyoke College, unpublished data).

METHODS AND RESULTS

Dispersal—Seed dispersal distances were estimated using seed traps arrayed in a regular pattern around five isolated (no other flowering plants within a 2.5 m radius) focal plants each with a single maturing capsule. In early October 1998, prior to dehiscence and dispersal, we arrayed 25 10 × 10 cm

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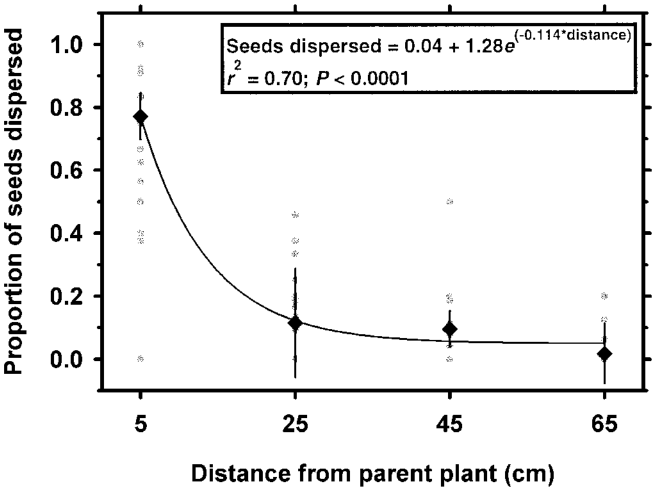

Fig. 1. Dispersal curve for *Sarracenia purpurea* seeds. Grey dots are raw data for each seed trap; solid diamonds are means, and error bars are ±1 SD of the mean. Line is the best-fit, three-parameter negative exponential curve.

plastic plates coated with Tanglefoot (Forestry Suppliers, Jackson, Mississippi, USA) in four concentric circles, 5, 25, 45, and 65 cm, from each target plant (method after Rabinowitz and Rapp, 1980). From 16 October through 3 December we counted the total number of seeds on each plate weekly. Most seeds had dispersed and snow covered our plates by mid-December. In total, only 200 seeds were caught on the traps; this represents only approximately 10% of the estimated seed production of these five plants. Most seeds (78%) recovered were within 5 cm of the parent plant; the median dispersal distance was 5 cm, and the mean was 12.8 cm. The shape of the dispersal curve closely was fit by a relatively steep negative exponential curve (Fig. 1).

Establishment—The probability of successful seedling establishment was determined in two ways. First, we carefully examined the area around our 1998 target plants in the summer of 1999 and counted all seedlings. We found a total of 338 seedlings around these target plants. Overall, the mean dispersal distance of these seedlings was 7.8 cm and the median dispersal distance was 1 cm. As with the dispersal experiment, the data were fit very well (r^2 = 0.99) by a negative exponential model.

Second, in October 1999 we planted five replicate plots of 100 seeds each on the *Sphagnum* mat. Seeds were planted just below the *Sphagnum* surface on relatively flat portions of the bog mat in regular 10 × 10 grids with 2-cm spacing between seeds. The plots' corners were flagged to allow for their relocation. We censussed these plots monthly during the 2000 growing season and again at the end of the 2001 growing season. Very few seedlings successfully established in these plots. Only one seedling was found in 2000, whereas in 2001 we found 20 seedlings (8, 1, 10, 0, 1, respectively, in the five plots). Based on these data, we estimate the probability of successful seedling establishment to be approximately 5%.

Does estimated dispersal and establishment mirror observed plant distributions?—If our estimates of average dispersal distance, shape of dispersal curves, and probability of establishment are realistic, we should see these values reflected in the spatial distribution of adult and juvenile plants. We therefore mapped all *S. purpurea* individuals in two 5 × 5 m plots at Hawley Bog. Each plant was located (±1 cm) using a Sonin electronic rangefinder (Forestry Suppliers) and the rosette diameter measured. Plants <10 cm in diameter were considered juveniles, and those ≥10 cm were considered adults, as we have never seen a plant <10 cm flower. We located 43 plants in plot 1 and 303 in plot 2. The smallest plants found had rosette diameters of 0.5–1 cm. Spatial clumping was assessed visually and by comparing the empirical distribution of plants to that predicted from a random (Poisson) process. Visualization and analysis were done with the SpatialStats module of S-Plus 6 for Windows (Insightful Corporation, Seattle, Washington, USA).

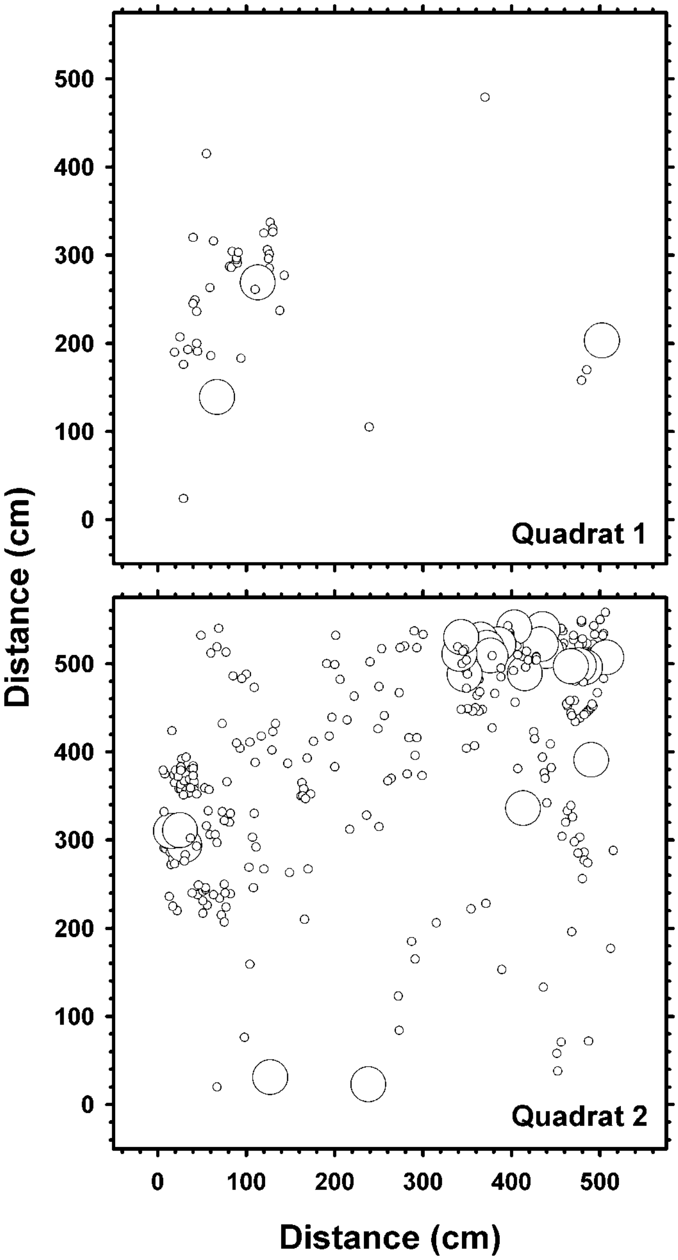

Fig. 2. Spatial pattern of juvenile (small circles) and adult (large circles) *Sarracenia purpurea* individuals in two 5 × 5 m exhaustively mapped quadrats at Hawley Bog.

In all plots, spatial clustering of plants was clear (Fig. 2). In both plots, significant clustering of plants occurred at spatial scales up to 200 cm ($P < 0.05$, based on Monte Carlo simulations of Ripley's K function [Ripley, 1976]). Additionally, in plot 2, we observed significant spatial autocorrelation in rosette diameters; large plants tended to cluster with other large plants, and small plants tended to cluster with other small plants (Moran's statistic = 3.4, exact $P = 0.006$). For plot 1, in which sample size was comparatively small, no significant spatial autocorrelation was observed (Moran's statistic = −0.09, exact $P = 0.47$).

Lastly, we simulated dispersal and establishment of *S. purpurea* using our estimated parameters for dispersal and establishment (C code for conducting these simulations is available on request from the first author). These simulations ($N = 100$) were not significantly different (exact $P = 0.45$) from the field observations in terms of spatial clustering (expressed as distance-to-nearest-neighbor and Ripley's *K*).

DISCUSSION

Like most herbs of woodlands, fields, and wetlands of North America (Cain, Damman, and Muir, 1998), *Sarracenia purpurea* seeds disperse over short distances (Fig. 1) and seedlings cluster together about the parent plant (Fig. 2). Based on controlled plantings, seedling mortality in the field appears to be high (approximately 95%). Although germination in laboratory conditions approaches 100% (Ellison, 2001), we did not estimate directly germination in the field. Rather, our estimate of establishment probability includes the unmeasured effects of seed predators, herbivory, and disease, among other post-germination risk factors. The observed negative exponential distribution of dispersal, and the observed clumping of plants suggests that seed dispersal is important in generating small-scale patterns of plant distribution. If small seedling mortality were nonrandom, the spatial patterns generated by seed dispersal models based on the negative exponential distribution would not match the field distribution of juveniles nearly as well.

Sarracenia seeds are very small, and they have no obvious ornamentation, eliasomes, or other structures to attract potential long-distance dispersers. Although seeds of *S. purpurea* are hydroscopic (A. M. Ellison, Mount Holyoke College, personal observation) and long-distance dispersal may be effected by flotation, the maximum dispersal distance recorded for another water-dispersed herb, *Mimulus guttatus* DC, is only 4 m (Waser, Vickery, and Price, 1982). If *S. purpurea* seeds dispersed by water have a similar dispersal distance, or even one that is 1–2 orders of magnitude greater, they are still unlikely to disperse easily between isolated bogs. Thus, the broad range expansion of *S. purpurea* since the end of the Pleistocene glaciation, from the southern coastal plains up the east coast of North America and across Canada to British Columbia, is explicable only by invoking rare, very long-distance transport events.

The population genetic structure of *S. purpurea* suggests that such long-distance dispersal events have occurred and have led to diversification by isolation. This taxon is normally divided into two subspecies, subsp. *purpurea* and subsp. *venosa*, with the former occurring northward from Maryland, just south of the limit of the Pleistocene glaciation, and the latter occurring from Maryland south (Schnell, 1979). Three disjunct varieties have been described for the southern subspecies: var. *venosa* (Raf.) Fernald that is found on the southern Atlantic coastal plain of the United States, var. *montana* Schnell & Determann that grows in the Appalachian Mountains of Georgia and the Carolinas, and var. *burkii* Schnell that is found only on the coastal plain of the Gulf of Mexico in Florida and Louisiana (Schnell, 1993; Schnell and Determann, 1997). The latter variety has been recently elevated to species status as *S. rosea* Naczi, Case & Case (Naczi et al., 1999). These disjunct occurrences of the subspecies and varieties of *S. purpurea* correspond to genetic differentiation (Godt and Hamrick, 1998), morphological variation (Naczi et al., 1999), and differences in seed size and dormancy requirements (Ellison, 2001).

Throughout its range, however, *S. purpurea* occurs in isolated bogs. Rare long-distance dispersal events could have resulted in the distributional pattern of subspecies and varieties if diversification occurred in peripheral bogs following dispersal. Seed size and dormancy vary little within a subspecies or variety (Ellison, 2001), but genetic and morphological differentiation within and among populations of each subspecies and variety have not been investigated. Such studies are needed to assess the prevalence of founder effects in this species, with an eye towards determining the genetic variability among bog plants generally. The occurrence of so many isolated populations of a single taxon presents a unique challenge to any general theory of long-range seed dispersal (e.g., Clark et al., 1998) and an opportunity to understand better the potential for species persistence in highly fragmented habitats.

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