

## Factors Controlling the Distribution and Abundance of the Narrow Endemic, *Helenium virginicum* (Asteraceae): Antiherbivore Defense?

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### INTRODUCTION

*Helenium virginicum* Blake, the Virginia sneezeweed, is a perennial herbaceous member of the Asteraceae that is globally endemic to about 22 sinkhole ponds in Augusta and Rockingham Counties, Virginia (Knox, 1995; Van Alstine, 1996). The state of Virginia lists the species as Endangered (Porter & Wieboldt, 1991), and the U.S. Fish and Wildlife Service has recently listed the plant as a Threatened species under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service, 1998).

The narrow endemism of *Helenium virginicum* seems to reflect its limitation to rare sites where competition with other species has been reduced by an unusual combination of stressful edaphic and hydrologic conditions (Knox, 1997). The clay soils at the sinkhole ponds where this species grows have a low pH, averaging 4.5, low levels of B, Ca, K, Mg, and P, and high levels of Al and As. The combination of low pH and high Al is the most important edaphic condition that limits the agricultural use of acid soils worldwide (Barinaga, 1997; Fuente et al., 1997), and is well known to impair uptake of the required macronutrients Ca, Mg, and K (Foy, 1974; Taylor, 1988).

Growing conditions in the sinkhole ponds inhabited by *H. virginicum* are made more stressful by dramatic seasonal changes in water depth (Fig. 1), with months of continuous flooding in cooler seasons alternating with periods of drawdown, when the basins lack any standing water, during warmer times of the year. Year-to-year variation in the duration of flooding may be great (Fig. 1); long periods of inundation have been associated with precipitous reductions in one population of *H. virginicum* (Fig. 2) intensively studied for 12 years at Kennedy Mountain Meadow (Knox, 1997; J. S. Knox, unpublished data). In other species, risk of extinction has been found

to increase with increasing stochasticity of the environment and increasing variability of population size (Goodman, 1987; Pimm et al., 1988; Menges, 1991). It is not surprising then, that the Kennedy Mountain Meadow population has twice crashed after unusually lengthy periods of inundation that lasted for 16 and 20 months, in 1989 - 90, and 1995 - 97, respectively. Each time that extinction of extant plants has occurred, recruitment from a seed bank regenerated the population within one month of drawdown. In each case, local extinction was associated with heavy growth of floating aquatic vegetation.

Evidence suggests that these local extinctions might be explained in part by the shade intolerance of *H. virginicum*. Knox (1997) found that distribution of *H. virginicum* plants within sinkhole basins reflected shade intolerance of the species. At sites surrounded by tall forest with a relatively dense canopy, plants were absent from the south side of the basins where shade is greatest. Knox (1997) observed that deeper sinkhole ponds tended to have *H. virginicum* plants distributed in a belt, beyond the shade of dense vegetation near the shoreline, but not too deep to experience too much shade from the water column during the winter period of inundation. Knox (1997) found that the patterns of natural recruitment and the survival of transplants at Kennedy Mountain Meadow also suggested that *H. virginicum* is shade intolerant. Also, viable seeds that have broken dormancy do not germinate under favorable temperatures when the seeds are in the dark or under a standing column of water that contains green plants (J. J. W. Harvey and J. S. Knox, unpublished data). The plant grows year round, as is evident from the more narrow leaves produced during winter inundation (J. S. Knox, personal observation). We hypothesize that local extinctions occurred after long-term inundation because *H. virginicum* plants growing on the bottom of the basin were shaded below their light compensation point by

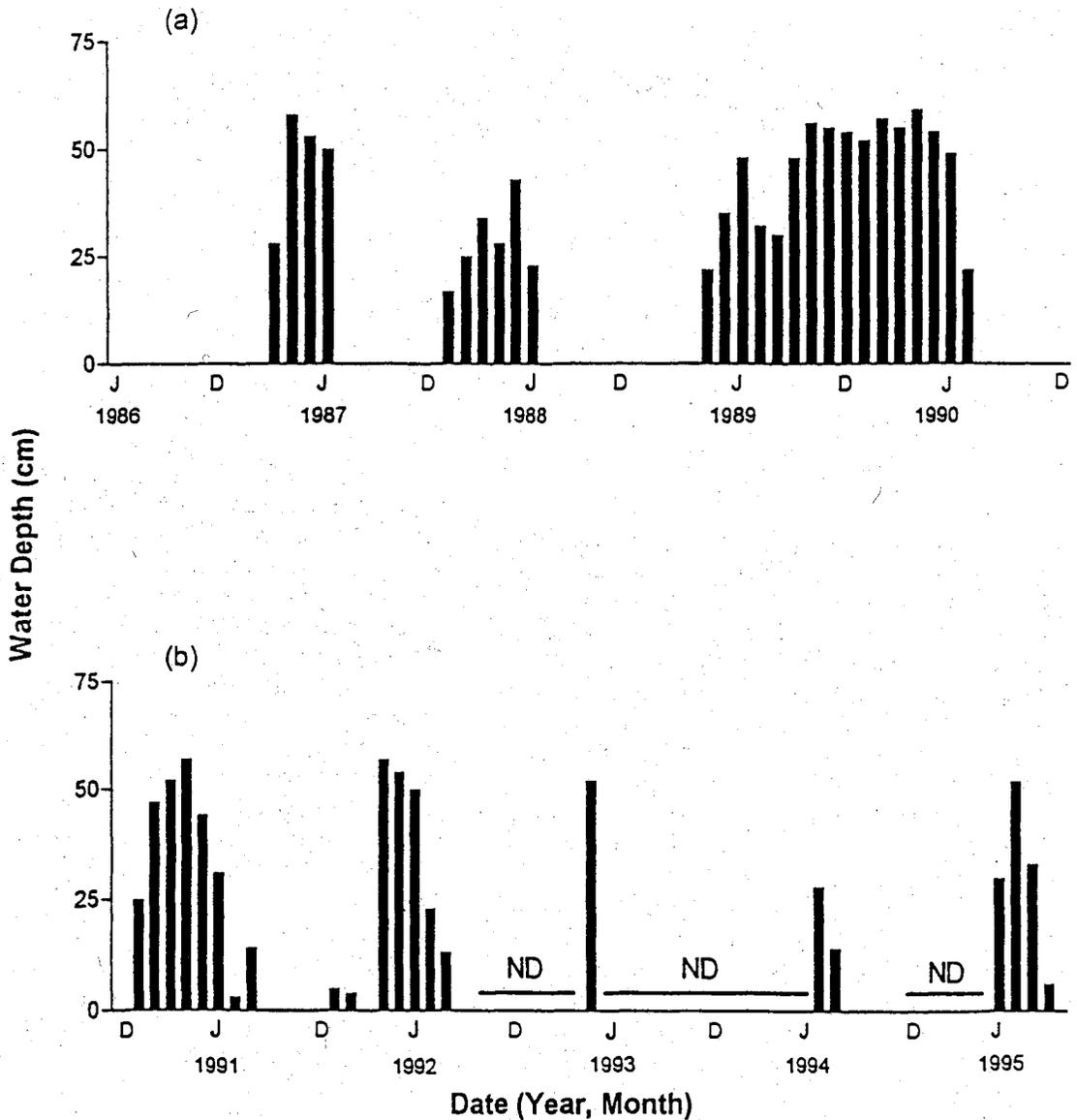


Fig. 1. Water depth (cm) measured monthly at the center (nearly the deepest point) at Kennedy Mountain Meadow. D is December; J is June; ND indicates no data collected.

floating aquatic vegetation.

Another factor that may make *H. virginicum* vulnerable to local extinction, and thus contribute to its narrow endemism, is the plant's sporophytic self-incompatible breeding system (Messmore & Knox, 1997). Successful seed production requires pollen with a different mating phenotype than is present on the stigma. Computer simulations (Byers & Meagher, 1992), as well as field studies (DeMauro, 1993) with other species, have revealed that this mating system increases the risk of local

extinction in cases where population size falls to fewer than 50 flowering individuals. We think that for *H. virginicum*, the high year-to-year variability in hydro-period, with its dramatic impact on population size, in conjunction with self-incompatibility, has created a situation in which the risk of local extinction is high and the probability of establishing a new population is low.

The largest and densest populations of *H. virginicum* occur at sites that have been disturbed by human activities such as mowing, grazing, and cutting trees. During a

period of population expansion in 1987, Knox (unpublished data) found densities of over 400 plants/m<sup>2</sup> at one sinkhole pond that had been disturbed by mowing, in comparison to densities up to 83 plants/m<sup>2</sup> at an especially dense area of an undisturbed site that same year. Knox (1997) speculated that the factors responsible for the much greater densities of *H. virginicum* at disturbed sites may have been activities that reduced the cover of competing plants, by trees having been cut, and the sites having been mowed and grazed. Knox (1997) called for future study of the impact of tree cutting, mowing, and grazing on *H. virginicum*, suggesting that this information could be useful for management of the species.

We suspect that *H. virginicum* may be unpalatable to herbivores; that grazing herbivores may selectively reduce the biomass of co-occurring plant species, thus reducing competition for light between the rare plant and its associates. This hypothesis seems plausible given that

other species of *Helenium* are known to be toxic and unpalatable to vertebrate (Hesker, 1982; Anderson et al., 1983) and invertebrate (Arnason et al., 1987) animals. The toxicity of *Helenium* (Anderson et al., 1986; Arnason et al., 1987) and other plant genera (Burnett et al., 1977) has been associated with sesquiterpene lactones. Since *H. virginicum* is known to contain a specific sesquiterpene lactone, Virginolide, (Herz & Santhanam, 1967), and handling the plant leaves a bitter residue on the hands (J. Knox, personal observation), we suspect that *H. virginicum* may be unpalatable to generalist herbivores.

To test this hypothesis, we established a common garden study site where native vertebrate herbivores were known to be common, and planted large numbers of *H. virginicum* in close association with large numbers of an attractant plant species palatable to those herbivores. We sought evidence of selective avoidance of *H. virginicum* by herbivorous animals that fed on adjacent attractant

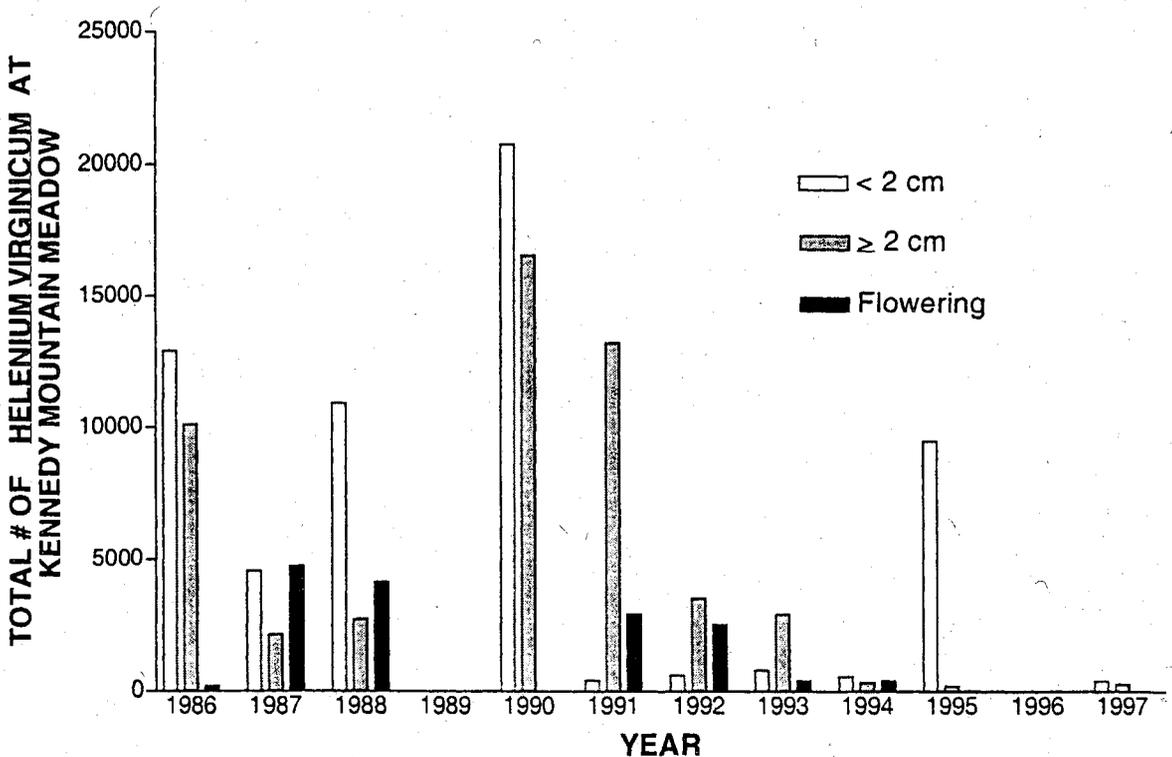


Fig. 2. Total number of *Helenium virginicum* plants growing within the 1 ha basin of Kennedy Mountain Meadow by stage class, censused in the fall of each year. Flowering refers to plants that flowered that season; < 2 cm refers to the length of the longest rosette leaf on plants that did not flower; ≥ 2 cm refers to the longest rosette leaf on plants that did not flower. Numbers are estimates made by extrapolating from annual census data taken at 53 permanent quadrats, except for 1994 and 1997, when total counts of all plants in the basin were made.

plants. We reasoned that if substantial herbivory of the attractant plant occurred, while interspersed with large numbers of *H. virginicum*, and the rare plant experienced little or no herbivory, we could infer that *H. virginicum* is unpalatable to herbivores. We were also interested to learn if *H. virginicum* would reduce the extent of herbivory on the attractant plant by comparing herbivory of attractant plants when grown in monoculture with those grown interspersed with *H. virginicum*. Such repellent plants have been described in other taxa (Atsatt & O'Dowd, 1976).

## MATERIALS AND METHODS

In May 1998, we established a common garden in the center of an old field of approximately 0.5 ha on the campus of Washington and Lee University, Rockbridge County, Virginia. This site was chosen because we had often observed native herbivores (whitetailed deer, *Odocoileus virginiana*; cottontail rabbit, *Sylvilagus floridanus*; and woodchuck, *Marmota monax*) in the field. We tilled a 15 m X 15 m plot and divided it into sixteen 2 m X 2 m quadrats arranged in a 4 X 4 block design. Quadrats were separated by a 1 m wide walkway that ran among them; a tilled zone of 2 m bounded the study plot. Between 22 May and 3 June 1998, we planted the quadrats with four replicates of each of the following four treatments. The control treatment (#1) contained 15 bean (*Phaseolus vulgaris*) plants and 15 *H. virginicum*, alternating by species, with a wire fence surrounding the quadrat to exclude large vertebrate herbivores. The fence was 1.25 m tall, had 2.5 cm X 2.5 cm mesh to a height of 30 cm, and 5 cm X 7.5 cm mesh above. The other three treatments were left unfenced so that vertebrate herbivores could have access to them. Treatment #2 was planted with 30 *H. virginicum*. Treatment #3 was planted with 30 bean plants. Treatment #4 was planted with 15 *H. virginicum* alternating with 15 bean plants. Treatments were arranged within each row of the plot in a regular sequence, with treatments staggered from one row to the next. We arranged the 30 plants in each quadrat in a grid of six by five plants, alternating by species, and on approximately 30 cm centers.

The *H. virginicum* plants used in this experiment were a cohort of 240 adult plants that had been raised in a common garden individually in 12.7 cm pots of Hyponex potting soils from seeds collected at one natural site, and were more than three years old. The attractant plants used were Burpee™ Stringless Greenpod bush beans, planted in two cohorts. The first cohort of bean plants was composed of 240 adult plants that had been raised individually in 12.7 cm pots of Hyponex potting soil in a greenhouse. When the first cohort of bean plants showed symptoms of

senescence on 5 June 1998, a second cohort of beans was started from seeds, by planting three bean seeds around each adult bean plant. On 17 June 1998, all first cohort bean plants were removed and the second cohort bean seedlings was thinned to leave one seedling where each first cohort bean plant had been. The treatment quadrats were weeded. We inspected the experimental plants nearly every day, but observed no evidence of herbivory until after the herbaceous vegetation in the surrounding old field was mowed on 6 July. On 8 July 1998, we began to observe substantial evidence of herbivory, and that evidence increased until 23 July, when we ended the experiment by harvesting the above ground biomass of each bean plant by cutting the stem at soil level. Each plant was placed separately in an aluminum pan and dried in an oven for three days at 95 C. Dried plants were placed at room temperature for one day, and then weighed to three decimal places on a top loading balance.

We tested for evidence of an herbivore repellent effect conferred by *H. virginicum* on the bean plants by comparing the above ground dry weight per bean plant under each treatment. We did this by using a Kruskal-Wallis nonparametric ANOVA to compare the median dry weight per bean plant for each treatment involving beans. The standard of  $P < 0.05$  was used to judge significance.

## RESULTS

When all beans were harvested and the experiment was concluded on 23 July, approximately 1/2 of all unfenced bean plants had been grazed with the top 10-25% of the bush removed. Many of the bean plants in all three treatments involving beans also showed evidence of insect herbivory, with leaf tissue having been partly removed between veins by Mexican Bean Beetles (*Epilachna varivestis*). None of the *H. virginicum* plants in any treatment had been grazed by vertebrate or invertebrate herbivores. We observed the hoofprints and feces of deer in the garden. The mean dry weight per bean plant  $\pm$  SD was  $5.04 \pm 3.76$  g for the fenced control treatment (#1) containing 15 beans and 15 *H. virginicum*,  $5.18 \pm 3.27$  g for treatment #3, the monoculture of 30 beans, and  $4.56 \pm 2.45$  g for the mix of 15 beans and 15 *H. virginicum*, unfenced. We found no significant difference ( $KW = 0.85$ ;  $P = 0.65$ ) in median above ground dry weight of bean plants in any paired comparisons.

## DISCUSSION

Our experimental data suggest that *H. virginicum* is unpalatable to the common vertebrate herbivores present on the campus of Washington and Lee University. When the rare plant was grown interspersed with beans, it

showed no evidence of herbivory despite substantial vertebrate herbivory on beans. The vertebrate herbivore that selectively grazed the beans and avoided *H. virginicum* seems to have been the whitetailed deer, judging from the deer hoofprints and feces found in the garden at the time herbivory was observed. It would be desirable to test the unpalatability of the rare plant at sites where it grows naturally and where cattle graze, by comparing the demography of plants in fenced and unfenced quadrats. Should *H. virginicum* be found to benefit from selective grazing of co-occurring species, conservationists might use this information to manage the plant. Although the Mexican bean beetle was a common invertebrate herbivore on beans, it is an insect that is host limited to members of the legume family, and therefore not a broad generalist herbivore. Thus, its absence from *H. virginicum* cannot be considered a special example of plant unpalatability.

The lack of significant difference between median dry weight of bean plants that had experienced vertebrate herbivory (treatments #3 and #4) and those that had not (treatment #1, the fenced controls) is puzzling. It is possible that the bean plants that had been grazed experienced compensatory regrowth of new tissue, such as has been observed in other plants (reviewed in Lennartsson et al., 1998).

Based upon all the available evidence presented here, we suggest the following conservation efforts and management practices for *Helenium virginicum*:

1. Protect the hydrology of the sinkhole ponds.
2. Discourage growth of floating aquatic vegetation by avoiding eutrophication.
3. Encourage measures that open sites to sunlight.
4. Permit grazing and/or mowing of sites on a trial basis, making comparisons between the demography of plants in fenced control plots and grazed or mowed plots within sites.
5. Facilitate gene flow between populations to reduce the risk of small population size to a plant with a self-incompatible breeding system.

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