Habitats of the Monkeyflowers
Mimulus alatus and *Mimulus ringens* on the Hudson River

by
Valerie Sharma
Polgar Fellow

Erik Kiviat
Supervisor
Bard College and Hudsonia, Ltd.
Annandale, New York 12504

ABSTRACT

Mimulus alatus, an emergent perennial of the family Scrophulariaceae, is ranked by the New York Natural Heritage Program as G5, secure globally, and S2, very vulnerable in New York State with typically 6 to 20 occurrences and few remaining individuals. Extant populations, ranging in size from 1 to 1400 plants, occur at ten sites within the Hudson Valley. To determine the specific habitat requirements of the species, as well as factors limiting its occurrence in this area, I worked at four local sites, three tidal and one nontidal, and tagged all stems in five populations. So that comparisons could be made with *Mimulus ringens,* a more common sympatric species, I tagged all stems in three populations at two of the tidal sites. I followed individual stems through the growing season to document phenology and demography. In early August 1992, I measured stem length, recorded presence of flowers, and documented mammal, insect, and mechanical damage; this was repeated six weeks later. To assess the effects of selected physical and biological factors on both species, I noted topographic position for each stem, measured soil pH and determined soil texture at each site, and estimated percent canopy cover over each population. I excavated one mature stem of each species to examine root system structure and depth of the rooting zone. I germinated *M. alatus* seeds indoors in an effort to gain information on sprouting conditions and growth potential.

Results from one field season showed that study populations of *M. alatus* found to be stable and most successful, based on greatest mean stem lengths and highest percentages of stems flowering, had several habitat affinities: mean canopy cover 58%-66%; limited disturbance, in the form of tides, runoff, or erosion; and slightly alkaline soil, usually sandy silt. Supratidal populations were more successful than intertidal or nontidal populations. Nontidal populations suffered substantial losses as a result of deer browsing. *Mimulus ringens* tolerated wider ranges of habitat conditions than *M. alatus.*

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Field studies contribute critical information on the habitat affinities of individual species (Gawler et al. 1987), and on the many factors that can threaten species survival (Menges 1986). In some instances, demographic monitoring is necessary to avert extinction (Travis and Sutter 1986). With knowledge comes increased ability to preserve extant populations (Baskin and Baskin 1986) and to establish new ones (Fitzgerald et al. 1990).

Genetic diversity allows a species to respond to changing environmental conditions. Local populations can contribute significantly to the overall fitness of a species. Thus it is important to manage small, local populations even when a particular species is existing at the edge of its range (Utter and Hurst 1990). Maintaining numerous local gene pools in reserves may be essential to effective conservation.

Mimulus alatus is ranked by the New York Natural Heritage Program as G5, secure globally, and S2, very vulnerable in New York State with typically 6 to 20 occurrences and few remaining individuals. Its legal status, according to New York State Environmental Conservation law, is R - rare; species listed as rare have 3,000 to 5,000 individuals statewide (Young 1992). According to the classification system of Rabinowitz (1986), *M. alatus* is habitat specific and widely-distributed geographically, with large populations at numerous sites in other states. Yet the species is ranked S3 by the Delaware, Kansas, and New Jersey Natural Heritage Programs - with 21 to 100 occurrences statewide, listed as highly vulnerable in Iowa and Nebraska, and classified as critically imperiled in Massachusetts and in Ontario, Canada. No definitive reason can be offered for the rarity of *M. alatus* at the northern edge of its range in New York.

Basic information on the life history of *M. alatus* is lacking. Habitat affinities are largely unknown, and limiting factors have not been studied. The sites of 4 of 10 known *M. alatus* populations in the Hudson Valley have been proposed for economic development.

The objectives of my study were:

- to determine the habitat affinities of *M. alatus* and some of the factors limiting its occurrence in the Hudson Valley region, using *M. ringens* for comparison;
- to assess the effects of selected physical and biological factors on both species by collecting data on canopy cover, topography, and soils;
- to follow plants of both species in order to document phenology and demography during one growing season;
- to investigate the feasibility of indoor seed germination of *M. alatus;* and

- to discuss possibilities for long-term species management.

Species and Study Area

Mimulus alatus and *M. ringens* are erect perennials of the family Scrophulariaceae. The rare sharp-winged or bird-winged monkeyflower is distinguished from the common or square-stemmed monkeyflower by the winged stem, leaves with petioles and coarse teeth, and shorter pedicel of the former (Figure 1).

Species exhibit neighboring sympatry (Lincoln et al. 1982) when they occupy different habitats within the same geographic area. Pennell (1935) stated that *M. alatus* and

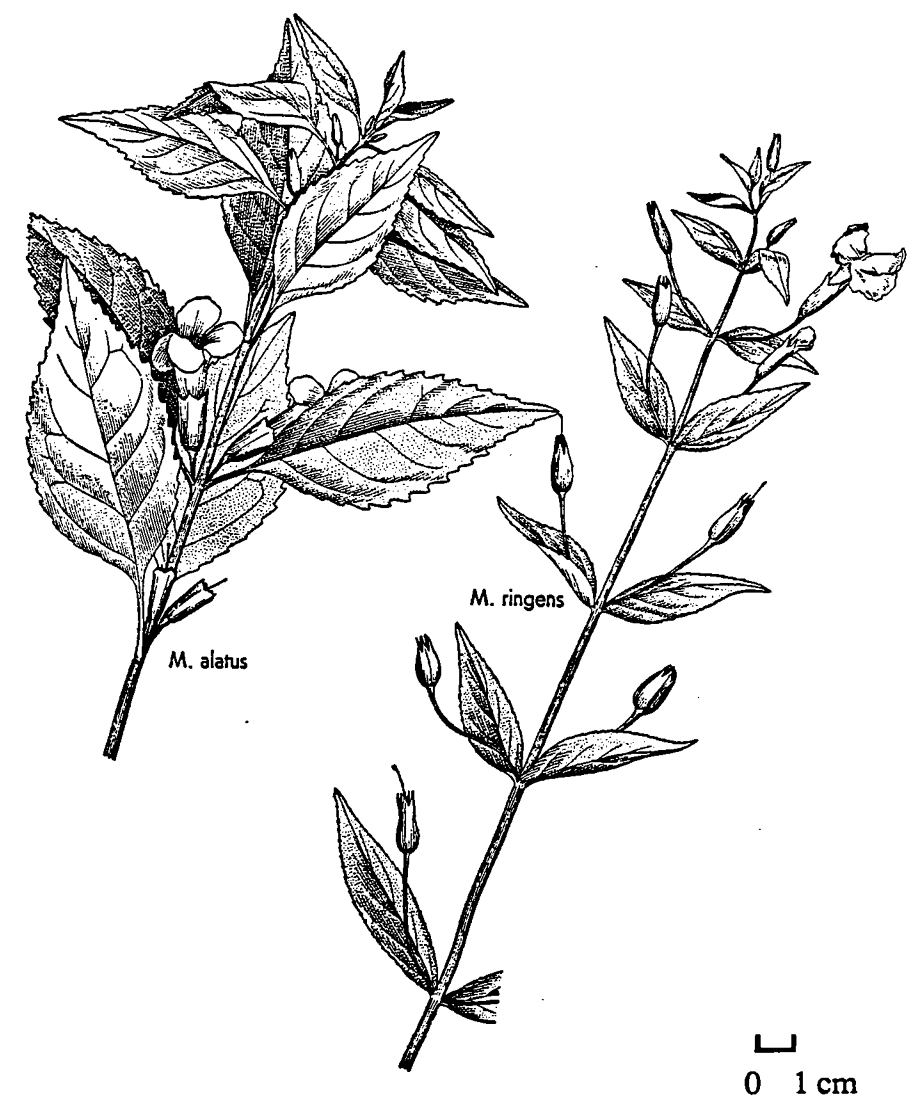
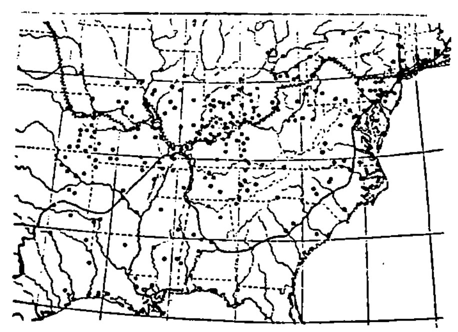


Figure 1. Morphology of *M. alatus* and *M. ringens* according to Gleason (1952). Reprinted by permission from The New York Botanical Garden, Copyright 1952.

M. ringens are sympatric over most of the eastern United States (Figure 2).

(a)



(b)

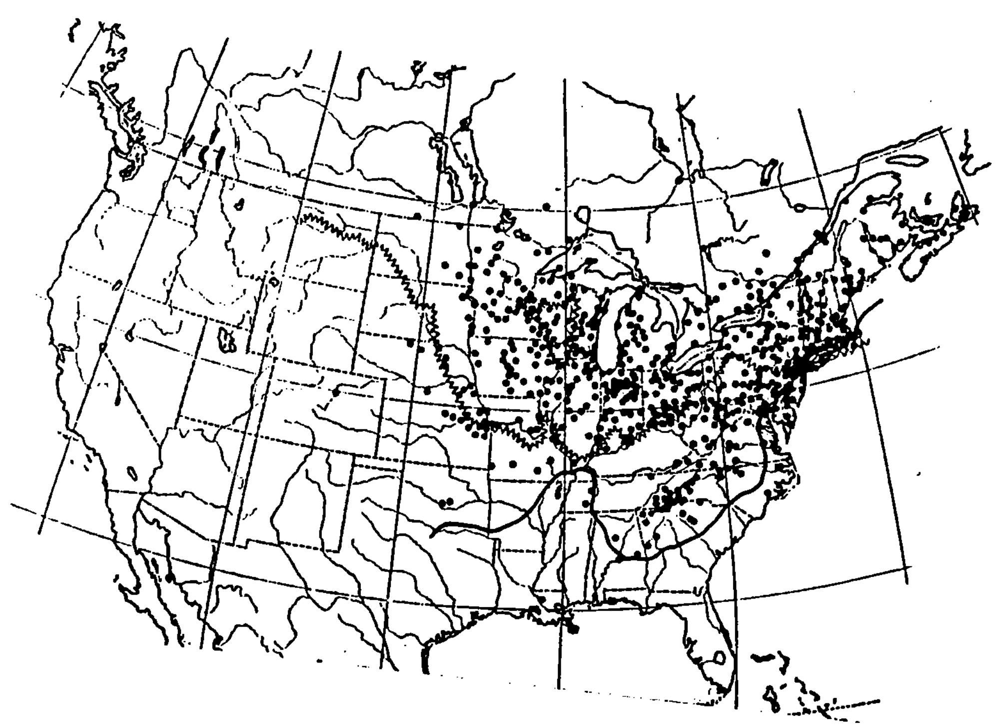


Figure 2. United States distributions of *M. alatus* (a) and *M. ringens* (b) according to Pennell (1935). Zigzag line is the southernmost extent of Pleistocene glaciation; solid line is the inner margin of the Atlantic Coastal Plain.

Mimulus alatus and *M. ringens* are among the few widely-distributed *Mimulus* species (Grant 1924). Sharp-winged monkeyflower is described as ranging from Connecticut to southern Ontario, southern Michigan and Iowa, and south to Florida and Texas, while common monkeyflower is found from Nova Scotia to Manitoba, south to Georgia, Alabama, and Texas (Gleason and Cronquist 1963). Both species are native to

eastern North America, where *M. alatus* occurs over much of the range of *M. ringens* (Cox 1985).

Within New York State, historical reports of the two species, compiled from herbarium specimens at the New York State Museum, show that the range of *M. alatus* has been significantly more narrow than that of *M. ringens*. Sharp-winged monkeyflower has been documented in only seven counties (Figure 3; New York Flora Association 1990), while common monkeyflower has been recorded in almost every one.

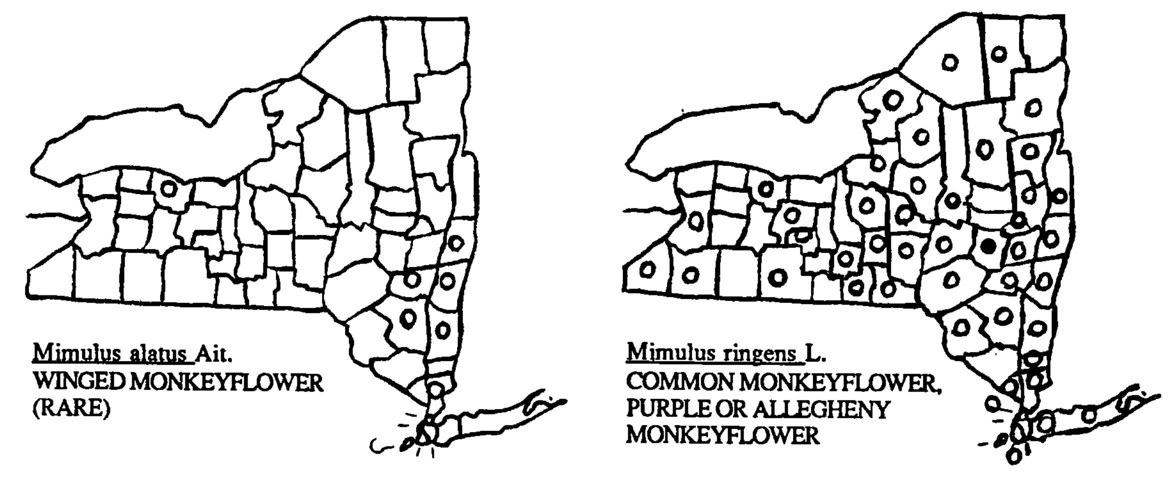


Figure 3. New York distributions of *M. alatus* and *M. ringens* according to the New York Flora Association (1990). Open circles = county records for species vouchered by pre-1980 specimens; solid circles = county records for species vouchered by 1981-1990 specimens.

Both *Mimulus* species occur in wooded wetlands, and *M. ringens* can also occur along streams (Britton and Brown 1913). Pennell (1935) characterized the habitat of both as "stream-banks, swales, and swamps, especially where alluvial or calcareous." Gleason and Cronquist (1963) stated that sharp-winged monkeyflower is found in wet woods, whereas common monkeyflower is more frequently observed on wet shores and in swamps, meadows, swales, and roadside ditches. Windler et al. (1976) generalized: "...*Mimulus ringens* occurs in open, marshy areas while *M. alatus* occupies shaded stream banks." Unpublished New York Natural Heritage Program data indicate that within the state, sharp-winged monkeyflower grows primarily in forested floodplain habitats.

Because both *M. alatus* and *M. ringens* are found only in wet habitats, Grant (1924) suggested that seed dispersal most likely takes place in mud carried on the feet of birds. Robert Zaremba (New York Field Office of the Nature Conservancy, Albany, NY, pers.

comm.) has described the sharp-winged species as opportunistic, taking advantage of small openings along waterways in places where ice or erosion has exposed mineral soils, while common monkeyflower is most often interspersed with other species within a larger community. Erik Kiviat (Hudsonia, Annandale, NY, pers. comm.) has suggested that Hudson Valley habitats for *M. alatus* are somewhat calcareous but not necessarily underlain by carbonate rock. Stephen Young (New York Natural Heritage Program, Latham, NY, pers. comm.) has posited that temperature could be a limiting factor for local *M. alatus* populations, and for other populations of the species growing at the northernmost range margin. Although *M. alatus* is described as a perennial (Windler et al. 1976), observations of Ulster County, New York populations suggest that it may be a biennial (Spider Barbour, Hudsonia, Annandale, NY, pers. comm.).

Within the past four years, sharp-winged monkeyflower has been discovered or confirmed on 10 sites within the Hudson Valley: 5 in Dutchess County, 2 in Ulster, 1 in Orange, 1 in Ulster and Orange Counties, and 1 in Columbia County. Three of these 10 sites are freshwater tidal, affected by the waters of the Hudson River; others encompass streams or wetland habitat. Observed population sizes at these locations have ranged from 1 to approximately 1400 stems. At least 5 of the 10 sites support populations of *M. ringens* as well.

I studied 8 populations at 4 sites in northwestern Dutchess County. For the purposes of this report, actual site names have been replaced by generic ones for reasons of data security. Three of the 4 locations are currently protected, within nature or historical preserves. The sites are briefly described below:

Site 1 - This is a supratidal, irregularly-flooded delta at the mouth of a small, perennial stream that flows into a tidal wetland of the Hudson River. The area is approximately 40 m x 20 m, following the shoreline. *Mimulus alatus* occurs under a deciduous canopy, partially composed of dead or dying trees.

Site 2 - This bay along the Hudson River is the location of two subsites. Site 2A is a rocky, intertidal shoreline that supports a population of *M. ringens;* the largely unshaded study area is approximately 60 m x 3 m. Site 2B is the 2 m wide channel of a small, perennial stream that extends from a waterfall through a cattail (*Typha*) marsh into the Hudson River. The population locations in the shaded, upper portions and the more open lower portions of the 60 m x 3 m site are both supratidal. *Mimulus alatus* and *M. ringens* co-occur here, the former along the entire length of the channel on both northern and southern banks, and the latter within 1 m^2 on the northern bank of the lower channel.

Site 3 - Two populations of *M. alatus* are found in nontidal habitats at this site. Site 3A is a shaded, southern stream bank near the base of a waterfall, while Site 3B is the edge of an old, silted eutrophic millpond where a dense hemlock (*Tsuga canadensis*) canopy dominates. The streamside population occurs within an area roughly 6 m x 1 m; the second population occurs intermittently around the pond in a band approximately 100 m x 1 m.

Site 4 - The most dominant features at Site 4 are the intertidal mudflats that line the lower banks of a small, sluggish stream near its mouth at the Hudson River. *Mimulus alatus* is found in the intertidal and supratidal zones, along a section of stream bank approximately 150 m x 3 m on both eastern and western sides. *Mimulus ringens* occurs along the same stretch, but only in the intertidal zone. Portions of the stream are bordered by deciduous woods to the east and a red cedar (*Juniperus virginiana*) glade to the west, resulting in an intermittently dense canopy throughout.

The freshwater reach of the Hudson estuary is characterized by a bimodal tidal cycle with a mean range of 1.2 m. The bedrock geology of the area and at all sites is the Austin Glen Formation, comprising graywacke and shale. The mainland is largely Hudson and Vergennes soils formed on deep, loamy or clayey, lacustrine materials, with areas of Knickerbocker formed on fine sandy loam from deep outwash (United States Department of Agriculture Soil Conservation Service 1991).

The area receives approximately 1021 mm of annual precipitation, of which 476 mm fall during a typical 150 d growing season extending from 1 May to 1 October. During this period, mean monthly temperatures range from 15.9 C to 23.7 C (Pack 1972). Spring and summer 1992 were unusually cool and dry. According to data from the Poughkeepsie FAA Weather Station (National Oceanic and Atmospheric Administration 1992), ca 5 km from the Hudson River, deviations from normal of mean monthly temperatures, March through August, ranged from -1.7 C to -0.7 C. During the same months, deviations from normal in precipitation ranged from -24.4 mm to -2.3 mm, with the exception of July when the deviation was 93.5 mm.

METHODS

In February 1992, I obtained Element Occurrence Records and Site Survey Summaries for *M. alatus* from the New York Natural Heritage Program (700 Troy-Schenectady Road, Latham, NY 12110-2400). I later visited selected sites in Ulster and Dutchess counties in order to document the status of reported populations, and I explored designated areas as well as adjoining ones for populations of *M. ringens*. I verified the continued existence of *M. alatus* populations at Sites 1, 3A, 3B, and 4, and discovered a previously unknown population at Site 2B. I found *M. ringens* in isolation at Site 2A, and with *M. alatus* at Sites 2B and 4.

Beginning in mid-June 1992, as soon as positive identification of *M. alatus* and *M. ringens* shoots was possible, I thoroughly searched Sites 1, 2, 3, and 4, and tagged stems that were 5 cm or longer. (Stems <5 cm were deemed too fragile to be tagged). Searches were usually made with an assistant, especially when vegetation was dense or the area to be searched was extensive; several searches per site were made on different days. Population boundaries were delineated when no new stems could be found in any compass direction within 50 m of those already marked. At Sites 3A and 3B, two distinct populations occurred more than 50 m apart, in unique habitats, and the plants were noticeably different in size and frequency of flowering.

Because both species are known to propagate vegetatively as well as by seeds, I tagged and counted stems, that is, vertical shoots separated at ground level, rather than plants (Table 1). I used waterproof, serially-numbered tags, which I fastened to stems up

Table 1. Study sites and populations of *M. alatus* and *M. ringens*.

Site	Classification	Species	Number of stems
1	supratidal	*M. alatus*	457
2A	intertidal	*M. ringens*	133
2B	supratidal	*M. alatus* *M. ringens*	60 33
3A	nontidal	*M. alatus*	64
3B	nontidal	*M. alatus*	128
4	supratidal and intertidal	*M. alatus*	86
	intertidal	*M. ringens*	92

to 30 cm above the ground with nylon cord tied as loosely as was feasible. A total of 1,053 stems were thus identified.

During the week of 2 August 1992, at each of the 4 sites, I measured stem length to the nearest 0.5 cm with a meter stick, recorded presence of flowers (open corollas), and documented mammal, insect, and mechanical damage. During the week of 20 September, I collected similar data and also noted topographic position for each stem (Figure 4). At Site 1, I had to deviate from this scheme, as conditions above position 2 in the delta were unlike

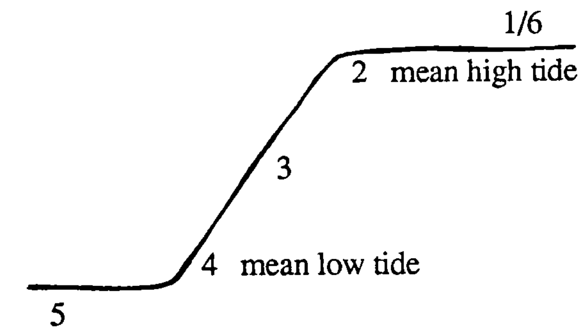


Figure 4. Topographic positions of *M. alatus* and *M. ringens*.

those at other sites. Tidal fluctuations combined with level surfaces at or just above mean high tide level result in soils which are saturated at shallow depths. Elsewhere, steeper slopes and higher elevations effectively prevent strong tidal penetration at the topographic position designated as 1. Consequently, at Site 1, in the delta, those stems above position 2 were assigned the number 6.

During the week of 23 August, I estimated percent canopy cover of plants taller than *Mimulus* at each site using a concave spherical crown densiometer (Robert E. Lemmon, Forest Densiometers, Bartlesville, OK, Model C). I placed the instrument at the tips of randomly-selected stems, counted dots representing exposed areas to a maximum of 96 for each compass direction, and then averaged these readings to obtain an estimate of the total exposed area above each stem. I multiplied these counts by 1.04 and subtracted the result from 100 to convert to estimates of percent canopy cover (Lemmon 1956). Counts were taken for a total of 205 stems. Random selection was achieved by use of a computer program which: eliminated browsed, broken, dead, and missing stems; generated a given number of stems (Table 2); and then specified a second set of stems to be drawn upon if

Table 2. Sample sizes for densiometer estimates of percent canopy cover.

Site	Species	Total stems	Sampled stems
1	*M. alatus*	457	50
2A	*M. ringens*	133	30
2B	*M. alatus* *M. ringens*	60 33	15 28
3A	*M. alatus*	64	15
3B	*M. alatus*	128	23
4	*M. alatus* *M. ringens*	86 92	20 20

previously-intact stems were damaged, dead, or missing.

During the week of 1 November 1992, I excavated a mature stem of each species to examine root system structure and depth of rooting. I dug trenches next to these stems, and sprayed water with an Indian pump and several sizes of wash bottles to disperse organic matter and soil. I mapped and photographed exposed roots. The excavated plants were deposited as voucher specimens in the Bard College Field Station herbarium.

I collected soil samples during the week of 15 November. For each population, I removed leaf litter, and with a garden trowel collected 10 samples, 5-10 cm deep, from spots 15 cm north of randomly-selected stems; as before, stems were randomly selected by computer. Samples were stored at room temperature for two hours. I measured the pH of each sample with an Orion SA 250 pH meter after mixing soil and distilled water in equal parts, stirring the mixture with a glass rod, and waiting for ten minutes (McLean 1982). A separate probe was used to compensate for differences in temperature. I then pooled the 10 samples per population, mixed the pooled samples well, and submitted a 1250 ml subsample from each pool to Empire Soils Investigations in Groton, NY for determination of soil texture.

Throughout the study, I made notes on plant condition, as well as any factors obviously affecting one or many individuals. I took 35 mm color slides to record life history changes. *Mimulus alatus* seeds collected from Site 1 during the week of 25 November 1991, and subsequently stored in a closed container and refrigerated, were germinated in Pro-Mix potting soil in mid-April 1992. Under a dissecting microscope I photographed seeds and seedlings grown indoors. Indoor specimens of different size classes were pressed and preserved as voucher specimens in the Bard College Field Station herbarium.

Data analysis was based on final stem length measurements and final documentation of flowering status. Populations with the greatest mean stem length and the highest percentage of stems flowering were determined. I compared these indicators of plant success with estimates of percent canopy cover, and with topographic position, soil pH, and soil texture. Comparisons were made among populations of the same species, between tidal and nontidal populations to the degree possible, and between species. I used Number Cruncher Statistical System, Student Version 5.0 (Hintze 1988) for data analysis.

One problem was encountered during the course of fieldwork. During the week of 20 September, when I measured stem length and recorded flowering status for the second time, even with intensive searching some stems could not be found; I was, therefore, unable to say with certainty whether they were surviving or dead. For the 8 populations, the percentages of stems unaccounted for ranged from 0 to 6.7 (<5.5% for 6 of 8

populations). In analyzing the data, I eliminated values for stems that could not be found, for stems known to be dead, and also for browsed stems, as including the latter could bias negatively both measures of plant success. I analyzed data from 615 *M. alatus* stems and 228 *M. ringens* stems. In an effort to evaluate the impact of browsing on study populations, I continued to follow browsed plants through the growing season; records kept make it possible to present browsing data.

RESULTS

Comparisons Among Populations

Measures of central tendency and variability varied greatly among populations (Table 3). Comparisons of stem length showed different population structures at all sites

Table 3. Measures of central tendency and variability for 5 populations of *M. alatus* and 3 populations of *M. ringens*. Stems were measured to the nearest 0.5 cm.

Site	Mean Stem Length (cm)	Median Stem Length (cm)	Range of Flowering Stems	Interquartile Range
		M. alatus		
1	46.6	44.0	20.5-107	44.0
2B	36.4	37.0	32.5-75.5	28.0
3A	32.2	25.5	35.5-86.5	25.5
3B	21.2	19.5	30.0-53.5	9.5
4	26.2	19.0	37.0-83.0	22.5
		M. ringens		
2A	22.8	19.0	14.5-69.5	16.5
2B	55.3	48.0	26.0-107	49.0
4	50.8	48.8	32.0-115	41.5

(Table 4). Sites 1 and 2B supported the only *M. alatus* populations with all size classes represented and many stems in each. Sites 3A, 3B, and 4 had fewer stems taller than 40 cm. Populations of *M. ringens* with all size classes represented and many stems in each occurred at Sites 2B and 4. The population at Site 2A also had fewer stems taller than 40 cm.

Based on mean stem length, and the highest percentage of stems flowering (Utter and Hurst 1990), the best sites for *M. alatus* were Sites 1 and 2B, and for *M. ringens*, Sites 2B and 4 (Table 5). If it is assumed that adult stems are those that flowered (Fitzgerald

Table 4. Comparisons of stem length for 8 *Mimulus* populations (20 September 1992). Data are percentages for each site.

Site	Size Class Midpoint (cm) 5	15	25	35	45	55	65	75	85	95	105	115
						M. alatus						
1	2.0	16.1	17.1	10.2	9.5	10.0	12.5	9.7	8.2	3.3	1.3	
2B	2.7	24.3	13.5	18.9	16.2	13.5	2.7	8.1				
3A	5.4	29.7	27.0	10.8	5.4	5.4	5.4	5.4	5.4			
3B	2.7	49.3	32.0	12.0	2.7	1.3						
4	2.7	49.3	16.0	14.7	6.7	5.3	2.7	1.3	1.3			
						M. ringens						
2A	7.2	45.6	22.4	16.0	2.4	4.8	1.6					
2B	0.0	8.0	16.0	16.0	12.0	8.0	4.0	12.0	8.0	4.0	12.0	
4	1.3	10.3	19.2	10.3	10.3	14.1	9.0	10.3	5.1	7.7	0.0	2.6

Table 5. Mean stem length and percentage of stems flowering for 8 *Mimulus* populations.

Site	Mean Stem Length (cm)	# of Stems Flowering Per Population	% of Stems Flowering Per Population
	M. alatus		
1	46.6	236/391	60.4
2B	36.4	21/37	56.8
3A	32.2	11/37	29.7
3B	21.2	10/75	13.3
4	26.2	11/75	14.7
	M. ringens		
2A	22.8	40/125	32.0
2B	55.3	18/25	72.0
4	50.8	41/78	52.6

et al. 1990), then the percentages of adult stems were much lower at *M. alatus* sites 3A, 3B, and 4, and at *M. ringens* site 2A.

A stable population has a greater chance of maintaining itself over time. The term "stable" can be applied to a population of a species when the population distribution includes all life cycle stages and many individuals in each (Baskin and Baskin 1986); however this is only true for species that reproduce strictly sexually. *Mimulus alatus* and *M. ringens* are known to reproduce sexually and also vegetatively (Figures 6-7), by structures which Gleason (1952) referred to as stolons and rhizomes. Thus, technically speaking, because I did not monitor vegetative reproduction, the term "stable" cannot be applied to my study populations.

Yet during this study of *M. alatus* and *M. ringens*, stolons were never observed in the field. In rare cases fragmentation was noted; broken stems developed roots at nodes and these roots then anchored new plants. When a plant of each species was excavated, short rhizomes were obvious on both; these were horizontal stems below the soil surface (Radford et al. 1974) bearing roots along their lengths and scale leaves near their tips, which in *M. alatus* protruded above ground level. But little can be said with certainty about rate of vegetative growth by rhizomes, as the species have not been well studied. Whether the short rhizomes evident on excavated plants would survive the effects of winter, insects, and other natural forces to give rise to spring shoots, can only be determined by further studies.

Comparisons of stem length for *M. alatus* at Sites 1 and 2B, and *M. ringens* at Sites 2B and 4, show all size classes represented with many stems in each; numbers and percentages of stems flowering indicate that many adult stems are present in these populations. Therefore, it is assumed that these populations have a greater chance than the other study populations of maintaining themselves over time - at least through sexual reproduction. So for the purposes of this paper, these populations will be termed "stable."

Estimates of percent canopy cover over the five *M. alatus* populations and the three *M. ringens* populations indicated distinct differences among the habitats (Table 6). For

Table 6. Estimates of percent canopy cover over 8 *Mimulus* populations.

Site	Mean Cover (%)	Range of Cover (%)
	M. alatus	
1	65.1	42.0-89.1
2B	58.1	27.2-88.6
3A	85.7	78.2-92.5
3B	89.8	84.4-96.1
4	92.7	83.1-97.9
	M. ringens	
2A	51.8	15.2-81.5
2B	40.8	18.6-62.8
4	62.4	4.8-95.8

M. alatus, two distinct groups were evident: populations with mean cover 58%-66%, and those with mean cover 85%-93%; the former group comprised the two populations already termed stable and most successful. For *M. ringens*, no such dichotomy was obvious. The two populations termed stable and most successful, at Sites 2B and 4, occurred in habitats with the lowest and highest percentages of mean cover respectively. The percentage of mean cover for the population at Site 2A fell almost squarely in between these low and high percentages.

Site-specific analysis of topographic position for *M. alatus* and *M. ringens* stems showed variable ranges at all locations (Table 7). For the *M. alatus* populations termed stable and most successful, at Sites 1 and 2B, the highest percentage of stems occurred in positions 6 and 2 respectively; the highest percentage of stems flowering occurred in these same two positions. At the other three sites (3A, 3B, and 4), the highest percentage of stems occurred in position 3. This is the position most likely to be affected by tides, runoff,

Table 7. Percentages of stems per population, by topographic position, at *Mimulus* study sites. Percentages of stems flowering, by topographic position, are underlined. See Figure 4 for topographic positions. NA = not applicable.

	Position					
Site	1	2	3	4	5	6
			M. alatus			
1	NA	11.5	19.4	3.3	3.3	62.4
	NA	<u>10.2</u>	<u>19.1</u>	<u>1.7</u>	<u>3.8</u>	<u>65.3</u>
2B	5.4	64.9	24.3	5.4	0.0	NA
	<u>9.5</u>	<u>57.1</u>	<u>23.8</u>	<u>9.5</u>	<u>0.0</u>	NA
3A	0.0	0.0	75.7	13.5	10.8	NA
	<u>0.0</u>	<u>0.0</u>	<u>54.5</u>	<u>18.2</u>	<u>27.3</u>	NA
3B	0.0	0.0	94.7	4.0	1.3	NA
	<u>0.0</u>	<u>0.0</u>	<u>100.0</u>	<u>0.0</u>	<u>0.0</u>	NA
4	26.7	28.0	45.3	0.0	0.0	NA
	<u>27.3</u>	<u>54.5</u>	<u>18.2</u>	<u>0.0</u>	<u>0.0</u>	NA
			M. ringens			
2A	0.0	8.0	75.2	16.8	0.0	NA
	<u>0.0</u>	<u>12.5</u>	<u>70.0</u>	<u>17.5</u>	<u>0.0</u>	NA
2B	8.0	48.0	44.0	0.0	0.0	NA
	<u>11.1</u>	<u>44.4</u>	<u>44.4</u>	<u>0.0</u>	<u>0.0</u>	NA
4	0.0	65.4	34.6	0.0	0.0	NA
	<u>0.0</u>	<u>85.4</u>	<u>14.6</u>	<u>0.0</u>	<u>0.0</u>	NA

and erosion.

While Sites 3A and 3B are nontidal with gentle slopes, making the effects of these three factors less dramatic, Site 4 is strongly influenced by the tides. At this site, 45% of the stems were found in position 3, but 55% of the flowering stems - the highest percentage - occurred in position 2, at the top of the bank; stems flowered most frequently when they were at or above the mean high tide mark. This was the only site at which the topographic position of the highest percentage of stems did not correspond with the topographic position of the highest percentage of stems flowering.

For *M. ringens*, a similar dichotomy was evident. At Sites 2B and 4, termed stable and most successful, the highest percentage of stems occurred in topographic position 2. The highest percentage of stems flowering was found in the same position, while at Site 2B an equal percentage of flowering stems occurred in position 3. Only at Site 2B were these two topographic positions very close in proximity, as the stems in position 3 were found very high on an almost vertical bank. At Site 2A, where the population was found to be unstable and least successful, the highest percentage of stems and the highest percentage of stems flowering occurred in position 3. This position is most strongly subjected to bank erosion.

Soil pH measurements for each of ten soil samples per population revealed some site-specific differences (Table 8). The two stable and most successful *M. alatus* populations

Table 8. Soil pH for 8 *Mimulus* populations, based on 10 samples per population. Conversions to hydrogen ion concentrations [H+] allowed calculation of mean pH.

Site	pH Range	Mean [H+]	Mean pH
		M. alatus	
1	7.0-7.7	0.000000060	7.2
2B	7.3-7.8	0.000000031	7.5
3A	6.4-7.3	0.000000184	6.7
3B	5.9-7.5	0.000000364	6.4
4	6.5-7.2	0.000000207	6.7
		M. ringens	
2A	6.7-7.3	0.000000121	6.9
2B	7.3-7.6	0.000000034	7.5
4	6.5-7.9	0.000000148	6.8

occurred at mean pH 7.2 and 7.5. The sites supporting the unstable and least successful populations were characterized by mean pHs of 6.7, 6.4, and 6.7. For *M. ringens*, no clear pattern could be discerned. The stable and most successful population of this species also occurred in slightly alkaline soil conditions, but the other stable and successful population was found at Site 4, where the mean pH was 6.8. The unstable and least successful of the three populations studied grew where conditions closely paralleled those at Site 4.

Particle size analysis of pooled soil samples for each population indicated some consistency between stable and successful populations and soil texture (Table 9). At Sites 1 and 2B, *M. alatus* thrived in sandy silt; the species lagged in silty sand (with a trace of gravel) at Site 3A, and in silt and clay (with a little sand) at Site 4. Only at Site 3B did *M. alatus* fail to prosper in sandy silt. *Mimulus ringens* populations evidenced greater mean stem lengths and higher percentages of stems flowering, first in sandy silt, and next in silt and clay (with a little sand). This species was unstable and least successful in silty

Table 9. Soil texture for 8 *Mimulus* populations. Use of a soil texture triangle (Buol et al. 1980) allowed textural class determination. Soil descriptions follow the Unified Soil Classification System (American Society for Testing and Materials 1992).

Site	% Gravel	% Sand	% Silt	% Clay	Textural Class	Soil Description
			M. alatus			
1	1.4	17.9	29.5	51.2	clay	sandy silt
2B	1.6	28.6	26.7	43.1	clay	sandy silt
3A	7.4	43.0	26.8	22.8	loam	silty sand / trace gravel
3B	0.3	14.2	28.3	57.2	clay	sandy silt
4	0.0	8.7	31.4	59.9	clay	silt + clay / little sand
			M. ringens			
2A	14.5	47.5	18.9	19.1	sandy clay loam	silty sand / trace gravel
2B	0.0	22.5	33.4	44.1	clay	sandy silt
4	0.0	7.4	36.6	56.0	clay	silt + clay / little sand

sand (with a trace of gravel) at Site 2A.

Browsing by white-tailed deer (*Odocoileus virginianus*) affected flowering in some populations (Table 10). Beginning with stems tagged when work at the sites was first initiated, I computed percentages of the populations browsed by the end of the growing season, and counted the number of browsed stems that ultimately flowered. For *M. alatus*, the two populations at Site 3 were most greatly affected, with few of the browsed stems flowering before or after browsing; in fact, some of these stems were rebrowsed during the course of the growing season. For both *Mimulus* species, high and almost equal percentages of stems were browsed at Site 2B; there, however, browsing had less of an effect on flowering. At other sites, browsing on either species was minimal.

Tidal and Nontidal Populations

All study populations of *M. ringens* were tidal, but populations of *M. alatus* occurred at both tidal and nontidal sites. Three occurred along the Hudson River; the other two were found at 20 m elevation above the Hudson.

Comparisons of stem length (Table 4), mean stem length, and percentages of stems flowering by site (Table 5) showed that the only two stable *M. alatus* populations

Table 10. Deer browsing in 8 *Mimulus* populations.

Site	% of Stems Browsed	% of Browsed Stems Flowering
	M. alatus	
1	4	29
2B	20	67
3A	38	9
3B	38	4
4	5	25
	M. ringens	
2A	2	67
2B	19	67
4	9	38

occurred at Sites 1 and 2B, both tidal sites; this does not imply that tidal populations are more stable than nontidal ones, however, as the three remaining unstable populations included one tidal and two nontidal sites. Based on mean stem length and percentage of stems flowering, populations at Sites 1 and 2B were also clearly the most successful ones. Additional exploration of this fact revealed some relevant points.

At Sites 1 and 2B, most stems occurred in topographic positions 6 and 2, respectively, where the highest percentages of flowering stems were also found. While the delta at Site 1 is tidally affected, tidal fluxes yielded few obvious changes in the microhabitat. Similarly, at Site 2B, *M. alatus* grew primarily at or above mean high tide, where tidal effects were generally less apparent. These were the only two supratidal sites.

At Sites 3A, 3B, and 4, however, most stems occurred in topographic position 3, the position most strongly subjected to tides, runoff, and erosion; the effects of these forces were especially apparent at Site 4. While the highest percentages of flowering stems also occurred in this topographic position for the populations at Sites 3A and 3B, at Site 4 the highest percentage of flowering stems was found in topographic position 2, the position at the upper limit of tidal influence. Moreover, even though percentages of flowering stems were relatively high, the total numbers of flowering stems per population at these three sites were very low: 11 of 37 at Site 3A, 10 of 75 at Site 3B, and 11 of 75 at Site 4.

All sites included in this study were subjected to some degree of disturbance by natural forces. *Mimulus alatus* was most successful where the disturbance was limited.

For both *Mimulus* species, the effects of deer browsing were different at tidal sites as

compared to nontidal ones (Table 10). The highest percentage of stems browsed at a tidal site was 20, whereas the lowest percentage of stems browsed at a nontidal site was 38. Moreover, at tidal sites, the lowest percentage of browsed stems flowering before or after browsing was 25; at nontidal sites, the highest percentage was 9. In summary, at tidal sites stems were browsed less, and browsed stems also flowered more often.

Comparisons Between Species

Mimulus alatus and *M. ringens* co-occurred at Sites 2B and 4, allowing comparisons between species at these locations. Both species were stable and successful (Tables 4-5) at Site 2B, while only *M. ringens* could be so described at Site 4. Percentages of stems flowering were used as indicators of population success; mean stem length could not be used, as the two species normally differ in size.

Of the two species, *M. ringens* was considerably more successful at both sites (Table 11). At Site 2B, for *M. alatus*, the highest percentage of stems and flowering stems

Table 11. Interspecies comparisons of one measure of success and three measures indicative of habitat affinities.

Species	% of Stems Flowering	Mean Cover (%)	Topo. Pos. w/ Highest % Stems	Topo. Pos. With Highest % Stems Flow.
		Site 2B		
M. alatus	56.8	58.1	2	2
M. ringens	72.0	40.8	2 3	2 3
		Site 4		
M. alatus	14.7	92.7	3	2
M. ringens	52.6	62.4	2	2

occurred in topographic position 2; for *M. ringens*, equal percentages of flowering stems were found in positions 2 and 3, where almost equal percentages of stems occurred. (At this site, positions 2 and 3 were in close proximity, for the most part - just above and just below mean high tide, respectively). Whereas *M. alatus* grew intermittently along the north and south-facing banks of a stream channel approximately 60 m in length, *M. ringens* grew only along a 1 m stretch on a south-facing bank.

At Site 4, both species grew along a 150 m section of stream bank. *Mimulus alatus* stems occurred most frequently in topographic position 3, but flowered most frequently in position 2. Clearly the position of most frequent occurrence did not favor flowering. For *M. ringens*, topographic position 2 supported the highest percentages of both stems and flowering stems. Occupying topographic position 2 more often than position 3, *M. ringens* flowered more frequently than *M. alatus*. Thus *M. ringens* also proved potentially better-suited to maintaining itself from one season to the next.

Estimates of percent canopy cover showed that *M. ringens* occupied habitat with a mean cover of approximately 40% at one site and 63% at the other; for *M. alatus*, mean cover percentages were roughly 58% and 93%. As both *M. ringens* populations were shown to be stable and successful according to measures of mean stem length and percentages of flowering stems, it can be assumed that the ranges of cover reported here are beneficial to the species. Given that the two successful *M. alatus* populations included in this study grew under mean cover of 58% and 65%, and that the population at Site 4 was termed both unstable and unsuccessful, this could indicate that a mean canopy cover of 92% is too high. The *M. alatus* population at Site 4 could be too shaded for long-term species success.

Comparisons of soil characteristics indicated potential differences between the two species (Tables 8 and 9). At Site 2B, where both *M. alatus* and *M. ringens* were found to be stable and successful, pH range and mean pH for the two species differed only slightly, and soil texture was identical. Site 4 supported populations of both species under similar conditions; pH range and mean pH of the predominantly silt and clay habitat were virtually the same. However, at this site, the *M. ringens* population was found to be stable and successful, while the *M. alatus* population was termed unstable and one of the least successful. This could indicate that *M. ringens* is tolerant of a wider range of soil conditions.

Life History

Mimulus alatus seeds collected from Site 1 during the week of 25 November 1991 were germinated indoors in Pro-Mix potting soil in mid-April 1992. In May 1992, *M. ringens* seeds were collected from plants of the previous growing season at a non-study site. Under a dissecting microscope, seeds of both species were examined and photographed. Examination confirmed the detailed descriptions of Godfrey and Wooten (1981): "Seeds about 0.5 mm long, plump, terete, in outline somewhat falcate, a little larger at one end than at the other, pale amber with a few reddish very finely knobby striae, the red color sometimes interrupted, a tiny dark reddish knob on either extremity" (*M. ringens*) and "...seed about as in *M. ringens* but faintly reticulate, the knobby striae usually not reddish" (*M. alatus*). Close inspection also revealed that *M. alatus* seeds are

more rounded than the seeds of *M. ringens*; moreover, one end is pointed while the other is round, and tips (knobs) are brownish.

For indoor seed germination, the potting soil was kept consistently moist, and *M. alatus* seeds sprouted within 14 d. Once cotyledons were apparent, seed containers were kept in strong filtered sunlight, weak filtered sunlight, or under a Sylvania fluorescent 20 Watt tubelight (Model F20T12/GRO/WS) for eight hours per day. Those seedlings placed in strong filtered sunlight grew tall and sturdy most quickly. The first pair of true leaves appeared at 26 d. Drawings made at 60 d (Figure 5) showed seedlings at slightly

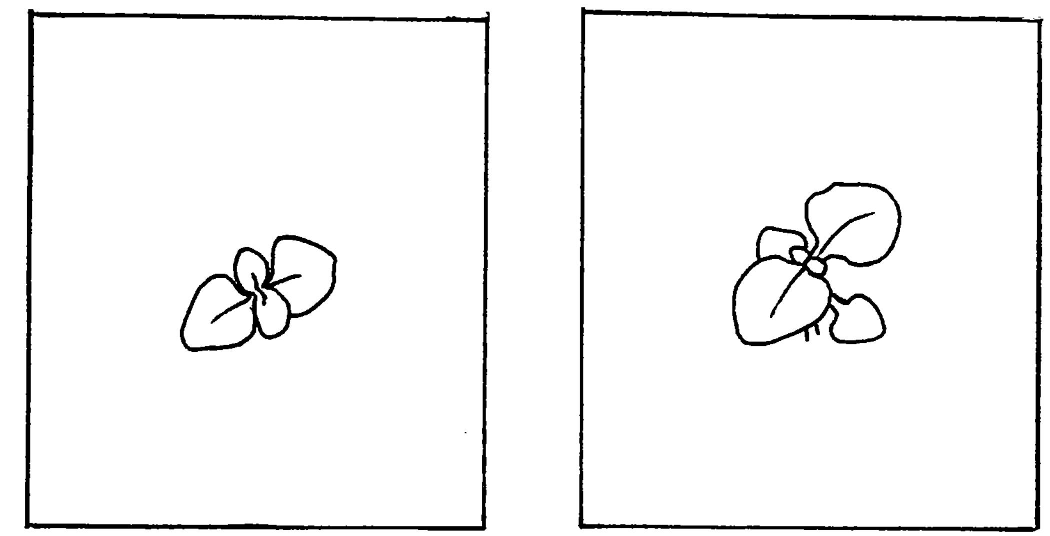


Figure 5. *Mimulus alatus* seedlings germinated indoors - at 60 d. The larger true leaves are 1.5 mm wide.

different stages of development. The 200 seedlings germinated were thinned in mid-July, and the strongest individuals transplanted to larger containers. Transplanted specimens grew successfully indoors to a height of approximately 10 cm. In September and October 1992, leaves and stems of individuals grown indoors began to senesce. Short rhizomes remain intact and continue to be monitored.

Positive identification of *M. alatus* and *M. ringens* seedlings in the wild was first made in mid-June 1992. Stems were approximately 15 cm tall. Tagging was completed and stems of both species were followed for one growing season. During this period, the following comparative observations of wild plants were made:

- *Mimulus alatus* flowers were open from July to September, but *M. ringens* bloomed only in July and August. Full-sized seed capsules were present on plants of both species by mid-September.

- While few insects were seen on plants of either species, signs of insect damage were recorded. At sites where *M. alatus* and *M. ringens* co-occurred, the *ringens* leaves more frequently had holes. A conspicuous white scale insect, identified by Jerry Jenkins, appeared at least twice as often on the rare monkeyflower as on the common one.
- Stems of *M. ringens* senesced earlier in the growing season than stems of *M. alatus*. For *M. ringens*, signs of wilting were detected as early as the last week in August. Many *M. alatus* stems appeared vital through the end of September.
- In mid- to late September, renewal buds (Daubenmire 1968) were noted protruding above the soil surface near the bases of most, if not all, *M. alatus* stems. I observed 2-8 buds per stem. Renewal buds were also obvious near the bases of seedlings grown indoors. Similar buds were rarely noted near the bases of *M. ringens* stems.

Excavations in the wild of one mature stem of each species were completed during the week of 1 November 1992. This made possible the examination of root system structure and depth of the rooting zone. The single specimens of *M. alatus* and *M. ringens* both had long underground stems of approximately the same length, but the two species used subterranean space differently (Figures 6-7).

Mimulus alatus rhizomes joined the underground stem at 4, 7, and 9 cm below the surface - deeper than *M. ringens* rhizomes which joined at 2, 4, and 5 cm below. The former were approximately 15 cm in length, whereas the latter reached 5-12 cm. Moreover the renewal buds of *M. alatus* protruded 1-1.5 cm above ground level; those of *M. ringens* extended only 1 cm, if at all. According to the life-form classification system of Raunkiaer (Daubenmire 1968), who emphasized proximity of overwintering buds to the soil surface, both species would be classified as hemicryptophytes. Hemicryptophytes require litter or snow cover for renewal bud protection.

DISCUSSION

This study has contributed considerable new information on *M. alatus*. Comparisons with *M. ringens* have placed both species in a broader context, which in turn has answered some questions and raised others; a one-year study necessarily bounds one in the present, without past or future knowledge to integrate with other findings. Yet, surely examination of both *Mimulus* species has suggested some possibilities for the long-term management of the rare sharp-winged monkeyflower.

Within the limited scope of this research project, *M. alatus* was stable and most successful in habitats where mean canopy cover was 58%-65%; the species was unstable

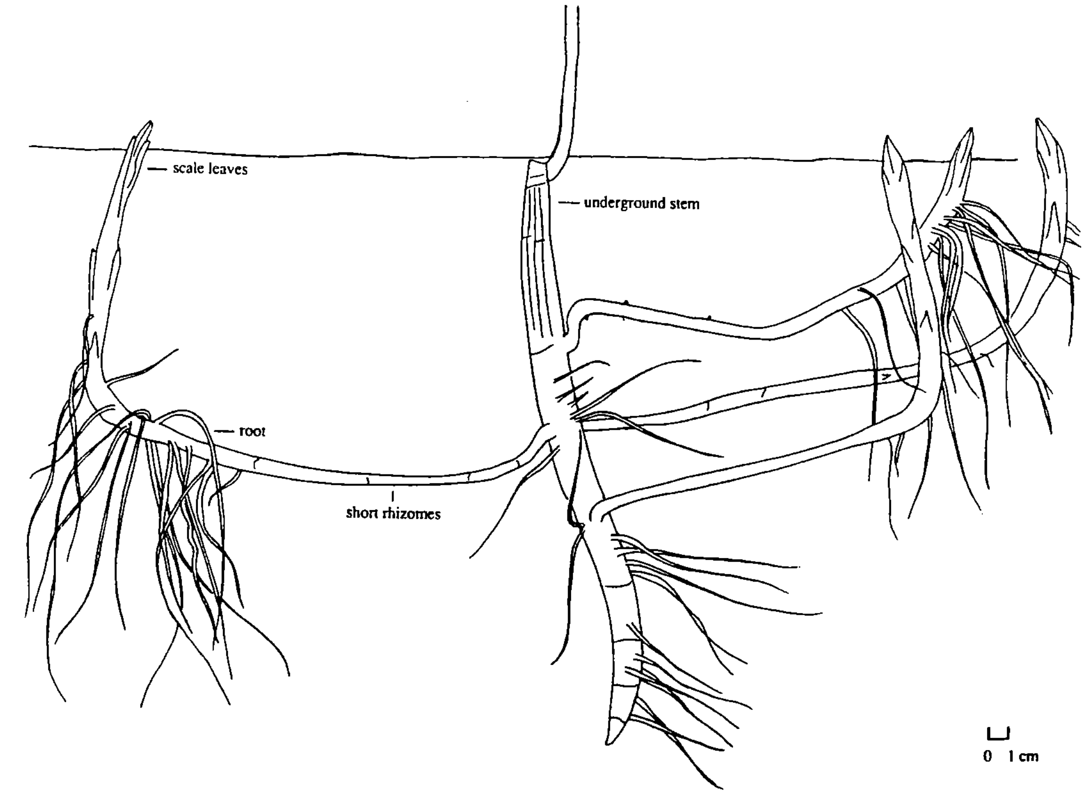


Figure 6 . Root system structure of a mature *M. alatus*.

and much less successful where the canopy exceeded 85%. Successful populations of *M. ringens* were found on sites with mean canopy cover of 41% and 62%; mean cover at Site 2A was 52%, probably conducive to species success, but this population presented itself as unstable and unsuccessful, most likely due to other factors. This study supports the generalization of Windler et al. (1976) that *M. ringens* occurs in more open areas than *M. alatus*.

All sites included in this study were known to be subjected to some degree of disturbance by natural forces, in the form of tides, runoff, or erosion. Of particular interest is the fact that in stable and successful *M. alatus* populations, the highest percentage of stems occurred in topographic position 2 or topographic position 6; in unstable and less successful populations of this species, the highest percentage of stems was found in topographic position 3, the position most likely to be strongly affected by bank erosion. As illustrated at Site 4, the degree of disturbance in position 3 actually may have worked against flowering.

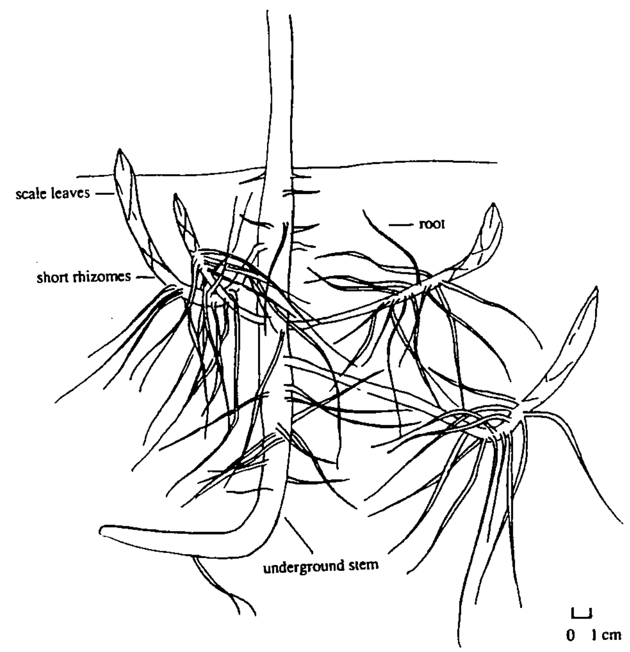


Figure 7. Root system structure of a mature *M. ringens*.

For stable and successful *M. ringens* populations, a similar generalization proved true. The highest percentage of stems occurred in topographic position 2. In the one unstable and unsuccessful population at Site 2A, the highest percentage of stems was found in position 3.

Mimulus alatus was most successful at sites where the degree of disturbance was limited; all stable and successful populations of the species occurred at supratidal sites. The sharp-winged monkeyflower may, therefore, be a "fugitive" species (Hutchinson 1951) - "restricted to periodically disturbed areas yet ... absent from areas of most extreme or most recent disturbance" (Gawler 1987). By contrast, *M. ringens* was stable and most successful at one supratidal site and at one intertidal site. This may indicate that the common monkeyflower can tolerate more disturbance than its rare congener.

Soil investigations showed that *M. alatus* thrived at the two sites where the mean soil pH was slightly alkaline - 7.2 at one and 7.5 at the other. The species lagged where mean pH dipped to 6.7 or below. Sites comprising less than 2% gravel, 14%-29% sand, 27%-30% silt, and 43%-57% clay supported the stable and most successful populations, with one exception; the population at Site 3B was unstable and least successful. The dense hemlock canopy and the low soil pH offer possible explanations.

Based on the small number of populations studied, *M. ringens* tolerated wider ranges of soil pH and differences in soil texture. The two stable and most successful populations occurred at sites with mean pH of 6.9 and 6.8, the first in sandy silt and the second in silt and clay (with a little sand). The unstable third population was considerably less successful in a habitat of silty sand (and a trace of gravel) with a mean pH of 6.9.

Finally, deer browsing was a limiting factor for *M. alatus* at some of the sites studied. At Site 2B, 20% of the stems were browsed, but 67% of the browsed stems were documented as flowering. At Sites 3A and 3B, much greater percentages of stems were browsed, some were rebrowsed, and less than 8% flowered before or after browsing. At sites such as these, browsing could severely limit seed production.

In summary, this study has shown that stable and most successful study populations of *M. alatus* had several habitat affinities: moderate light, with mean canopy cover of 58%-66%; limited, but not too much disturbance, such as that caused by bank erosion due to stream or tidal flooding; and slightly alkaline soil with the highest percentage of clay, followed by silt and sand. Tidal populations at supratidal sites evidenced the greatest mean stem lengths and the highest percentages of stems flowering. Nontidal populations may well need protection from white-tailed deer. Seedlings germinated indoors reached 10 cm, but transplanting to the wild was not attempted. Thus suggestions cannot be offered for use in mitigation or restoration projects.

QUESTIONS FOR FUTURE STUDIES

Certain objectives of this study have been accomplished more completely than others, particularly given the limitations of a single field season. Some of the habitat requirements of *M. alatus*, and a partial list of factors limiting its occurrence in the Hudson Valley region have been determined. The effects of certain physical and biological factors on the rare monkeyflower as well as the common one have been assessed. *Mimulus alatus* seeds have been germinated successfully indoors. Still there is much about the phenology and demography of the species that remains a mystery. Furthermore, information gained has given rise to new questions, as well as a desire to further develop the very limited understanding at hand.

The following questions remain for future studies:

- Do study populations remain stable and successful year to year? Do population sizes increase or decrease significantly over time? If so, why?
- Annually, for each species, how much recruitment comes from sexual as opposed to vegetative reproduction?
- Are *M. alatus* and *M. ringens* perennials or biennials?

- In natural settings, when do seeds of both species germinate?
- What percentage per species of renewal buds survives the winter? When does their growth commence? How many shoots survive until the end of the growing season?
- Do isotherms correlate with the range limits of these two *Mimulus* species?
- How much nutrient enrichment, siltation, scouring, stream flow variation, and sea level rise can these species tolerate?
- For *M. alatus* and *M. ringens*, what are the primary pollinators and insect pests?

While other questions might be asked, answers to these would go to the heart of maintaining the sharp-winged monkeyflower in the years to come. Surely, future generations should "see what appears to them the face of a little ape or buffoon (*mimulus*) in this ... flower whose drolleries, such as they are, call forth the only applause desired - the buzz of insects that become pollen-laden during the entertainment" (Blanchan 1900).

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