

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

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#### 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*.

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## 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 (Ulter 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).



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.

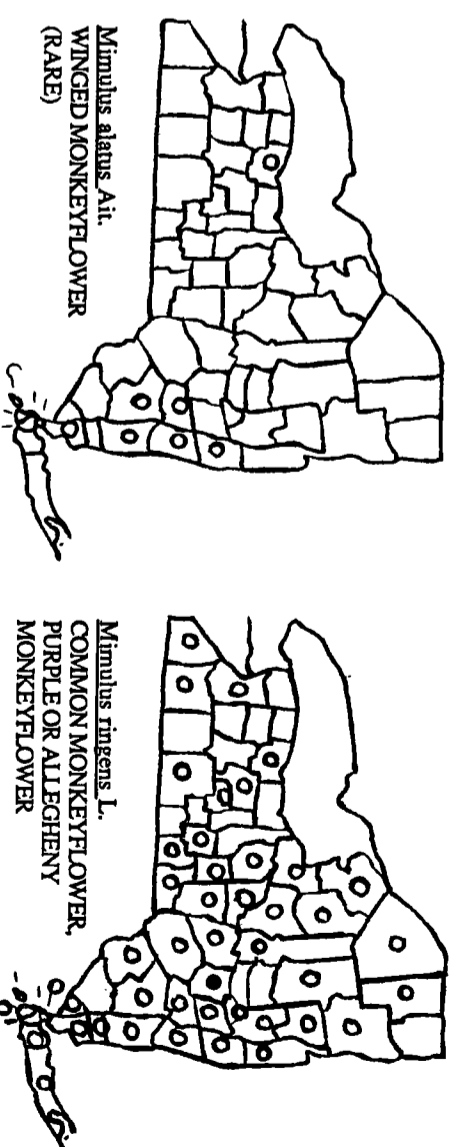


Figure 3. New York distributions of *M. alatus* and *M. ringens* according to the New York Flora Association (1990). Open circles = county records for species vouchered by pre-1980 specimens; solid circles = county records for species vouchered by 1981-1990 specimens.

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<sup>2</sup> 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	<i>M. alatus</i>	457
2A	intertidal	<i>M. ringens</i>	133
2B	supratidal	<i>M. alatus</i>	60
		<i>M. ringens</i>	33
3A	nontidal	<i>M. alatus</i>	64
3B	nontidal	<i>M. alatus</i>	128
4	supratidal and intertidal	<i>M. alatus</i>	86
	intertidal	<i>M. ringens</i>	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

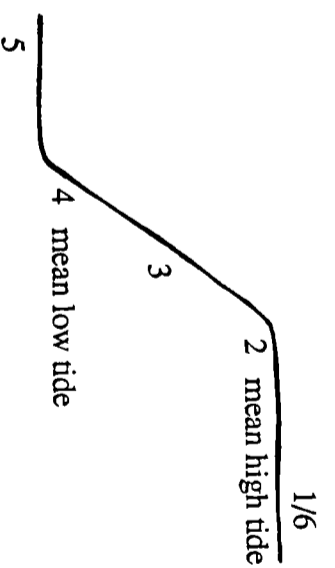


Figure 4. Topographic positions of *M. alatus* and *M. ringens*.

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 Densimeters, 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	<i>M. alatus</i>	457	50
2A	<i>M. ringens</i>	133	30
2B	<i>M. alatus</i>	60	15
	<i>M. ringens</i>	33	28
3A	<i>M. alatus</i>	64	15
3B	<i>M. alatus</i>	128	23
4	<i>M. alatus</i>	86	20
	<i>M. ringens</i>	92	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. *Minulus 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
<i>M. alatus</i>				
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
<i>M. ringens</i>				
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
<i>M. alatus</i>												
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			
<i>M. ringens</i>												
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

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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
<i>M. alatus</i>			
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
<i>M. ringens</i>			
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 (%)
<i>M. alatus</i>		
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
<i>M. ringens</i>		
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.

Site	Position					
	1	2	3	4	5	6
<i>M. alatus</i>						
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
<i>M. ringens</i>						
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 *Minulus* populations, based on 10 samples per population. Conversions to hydrogen ion concentrations [H<sup>+</sup>] allowed calculation of mean pH.

Site	pH Range	Mean [H <sup>+</sup> ]	Mean pH
<i>M. alatus</i>			
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
<i>M. ringens</i>			
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. *Minulus 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 *Minulus* 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
<i>M. alatus</i>						
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
<i>M. ringens</i>						
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 *Minulus* 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

